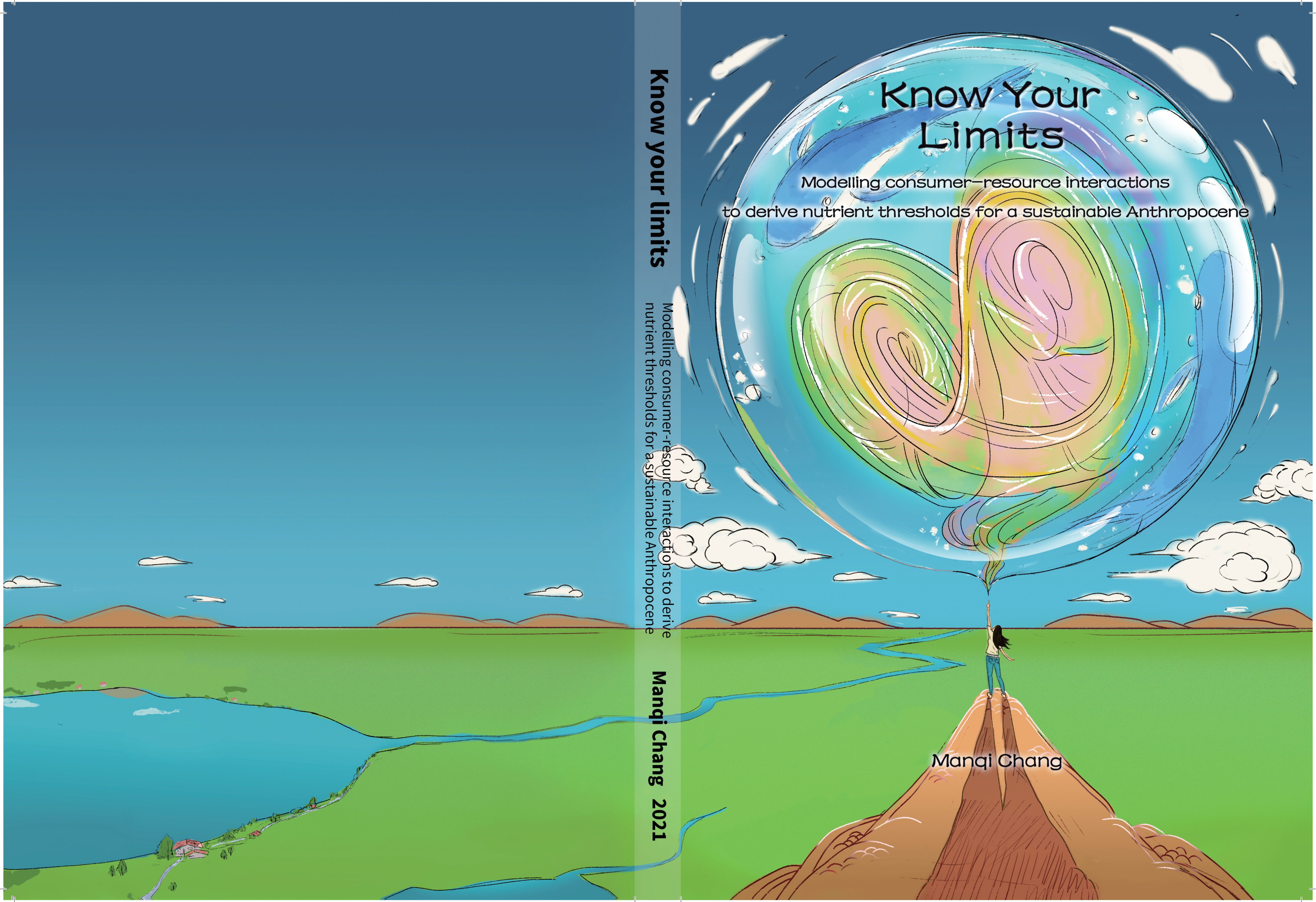

Know your limits

Modelling consumer-resource interactions to derive nutrient thresholds for a sustainable Anthropocene

Manqi Chang 2021

Know Your Limits

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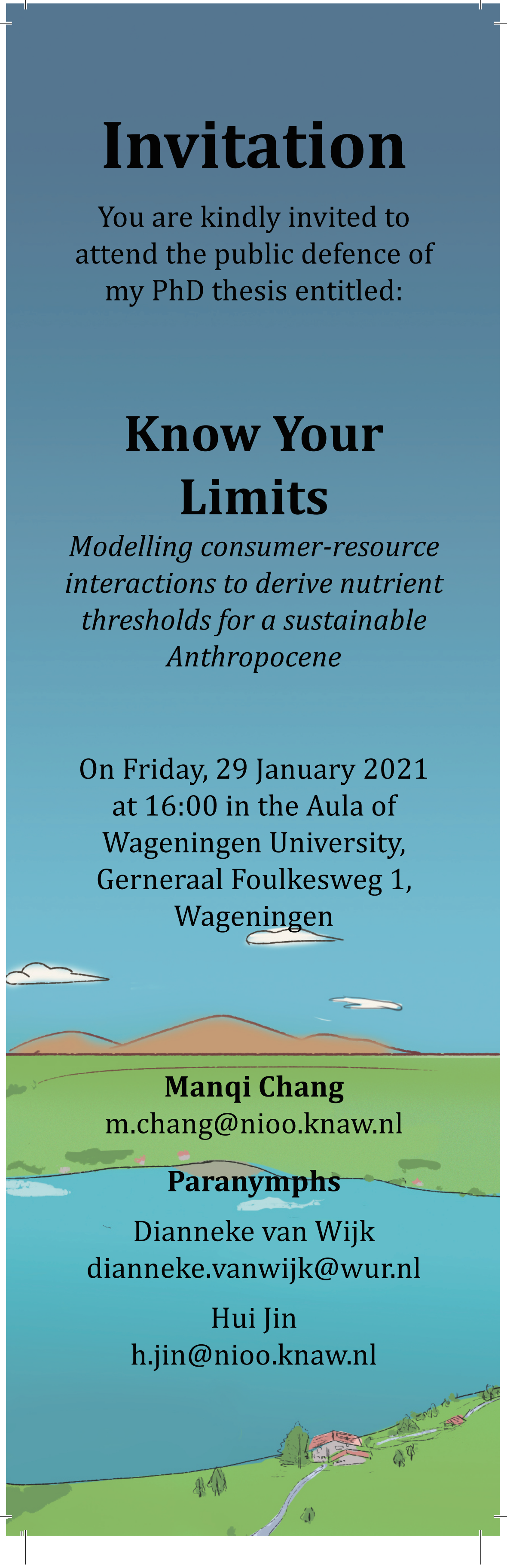

Invitation

You are kindly invited to attend the public defence of my PhD thesis entitled:

Know Your Limits

Modelling consumer-resource interactions to derive nutrient thresholds for a sustainable Anthropocene

On Friday, 29 January 2021
at 16:00 in the Aula of
Wageningen University,
Gerneraal Foulkesweg 1,
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Propositions

1. Mechanistic modelling is essential in reaching a sustainable Anthropocene. (this thesis)

2. Model developers should first focus on model functionality, not on realism. (this thesis)

3. Wrong predictions based on right reasoning are still preferable over right predictions based on wrong reasoning.

4. Limits are dynamic.

5. The way to tell the truth is as important as the truth itself.

6. Competence implies dealing with your incompetence.

Propositions belong to the thesis, entitled

Know your limits: Modelling consumer-resource interactions to derive nutrient thresholds for a sustainable Anthropocene

Manqi Chang
Wageningen, 29 January 2021

Know your limits

Modelling consumer-resource interactions to derive nutrient thresholds for a sustainable Anthropocene

Manqi Chang

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This research was conducted under the auspices of the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC)

Know your limits

Modelling consumer-resource interactions to derive nutrient thresholds for a sustainable Anthropocene

Manqi Chang

Thesis
submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus,
Prof. Dr A.P.J. Mol,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Friday 29 January 2021
at 4.00 p.m. in the Aula.

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谨以此书献给我的父母

This book is dedicated to my parents

Contents

Chapter 1

Introduction

1.1 Background

Eutrophication, or the enrichment with nutrients, has become one of the important reasons for the collapse of ecosystems on earth (Rockström et al., 2009a; Rockström et al., 2009b). Large input of nutrients to water bodies provide ample food for phytoplankton species to grow (Huisman et al., 2018). As a consequence, harmful species such as toxic cyanobacteria can become dominant, thereby outcompeting macrophytes, leading to oxygen depletion and related fish kill (Huisman et al., 2018). Thus, ecological functions of these aquatic ecosystems, such as providing biodiversity, clean drinking water, and recreational values to human society will be lost (Janssen et al., 2020). This collapse of ecosystems is accelerated by the prosperity of human society (Crutzen, 2006). Harmful algal blooms are prevailing worldwide (Glibert et al., 2005), especially in the populated and economically developed areas such as Europe (Jeppesen et al., 2007b), the U.S. (Baker et al., 2014), and Asia (Glibert, 2013; Fink et al., 2018; Tong et al., 2020). Intensive agricultural activities have satisfied the demand of the emerging population in the last century so that large amounts of fertilizers have been used and discharged to rivers, lakes and the ocean (Seitzinger et al., 2005; Strokal et al., 2016). Population aggregation due to urbanization generates large amounts of domestic sewage discharged into ambient aquatic ecosystems and causes serious health issues (Tong et al., 2020). Besides human activities, a warming climate and increasing extreme events such as storms can alleviate harmful algal blooms (Paerl et al., 2008; Perry, 2008; Wagner et al., 2009; Zhu et al., 2014). As a result, there is an increasing frequency of the occurrence of harmful algal blooms worldwide (Glibert et al., 2005; Huisman et al., 2018). Therefore, effective solutions for eutrophication management are urgently required for a sustainable supply of human needs while preserving ecological functions.

1.1.1 Sustainable development and environmental limits

The principle of sustainable development is to balance the current human need and the maintenance of natural resources and ecosystem services to ensure the demand for future generations (Raworth, 2017). In fact, the natural environment was much less suitable in much of the earth for human beings before the Holocene (Rockström et al., 2009a). During the Holocene, human beings gradually established agricultural and industrial systems to provide basic needs including food, clean water and shelter to guarantee population growth (Ponting, 1991). These developments allowed human civilization to thrive; however, development led to unfavourable environmental changes such as global warming, eutrophication, ocean acidification, air pollution, and biodiversity loss in recent centuries (Adrian et al., 2009; Rockström et al., 2009a; Herman et al., 2015). These environmental changes not only threaten humans but also threaten thousands of wild species on earth (Bar-On et al., 2018; United Nations, 2019). This era, which has been strongly influenced by human beings, has been named as the Anthropocene (Crutzen, 2002). The unfavourable environmental changes may soon reach a limit beyond which current ecosystems cannot recover (Rockström et al., 2009a). Therefore, one of the most important tasks in the Anthropocene is to define the environmental limits and take actions such as making regulations to indicate the acceptable level of pollution, to protect nature and maintain the sustainable development of human beings.

1.1.1.1 N and P limits in the concept of Planetary Boundaries

The Planetary Boundaries concept (Rockström et al., 2009a; Rockström et al., 2009b) is one of the most cited descriptions of environmental limits (Downing et al., 2019). In this concept, nine limits are defined as boundaries of a safe operating space within which both human development and ecosystem sustainability can be maintained (Rockström et al., 2009b). This concept of the boundaries is proposed on the basis of the theory that complex ecosystems are resilient, or in other words, that they have the ability of self-regulation, to remain unchanged until a limit is crossed due to strong perturbations (Holling, 1973; Scheffer et al., 2001). The qualification and quantification of these limits requires the understanding of the biogeochemical processes in the ecosystems.

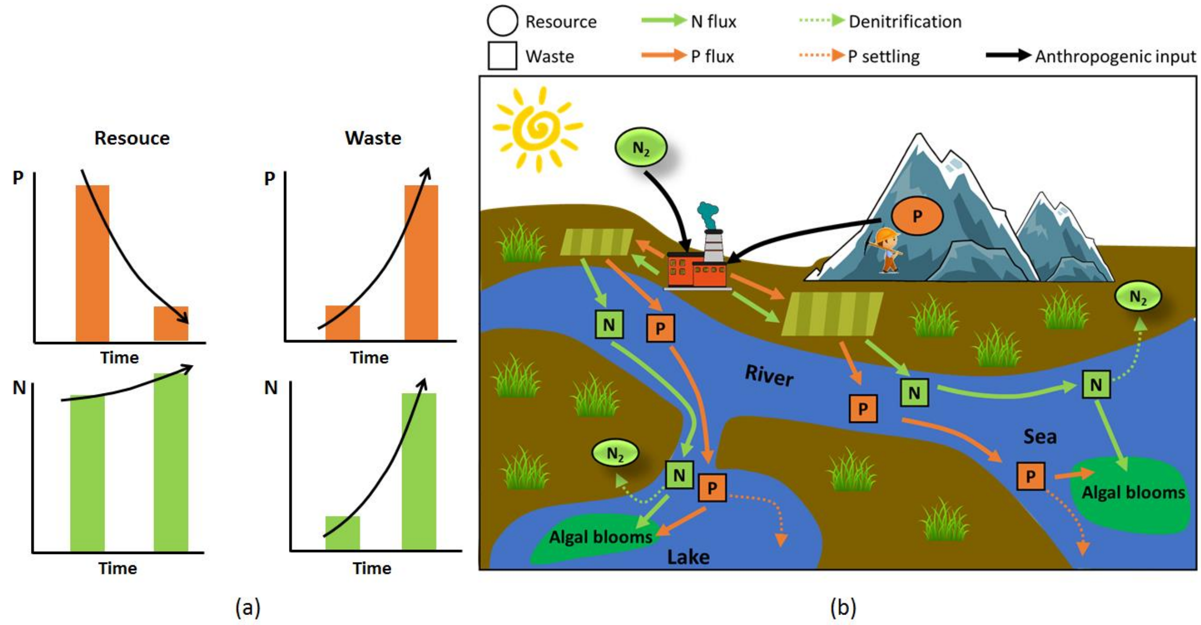


Figure 1.1 The conceptual figures for (a) Historical changes of N and P as resource and waste; (b) N and P cycles of showing how anthropogenic inputs generate waste in aquatic ecosystems.

Nitrogen (N) and phosphorus (P) cycles, defined as biochemical flows within the planetary boundaries, are one of the nine environmental limits, and both cycles are currently at high-risk (Steffen et al., 2015). Both N and P limits are defined according to the water quality criteria to prevent ecosystem collapse due to eutrophication (Carpenter et al., 2011; de Vries et al., 2013). The over-enrichment of N and P in aquatic ecosystems is due to the imbalance of the input and output of these resources (Figure 1.1). The anthropogenic input of N often comes from agricultural fertilizers that are produced by industrial nitrogen fixation (Galloway et al., 1995; Davidson, 2009). The resources of nitrogen may increase since atmospheric nitrous oxide (N_2O) has increased in recent centuries (Steffen et al., 2011). (Galloway et al., 1995; Davidson, 2009). The over-application of anthropogenic nitrogen as fertilizer leads to a large flux into aquatic ecosystems (Gruber et al., 2008). On the other hand, the resource of P can be obtained by mining industries or weathering of rock (Bennett et al., 2001; Carpenter et al., 2011). P is an unsustainable resource because much ends up in the sediments of freshwater or marine ecosystems, where some may be permanently lost (Liu et al., 2008). The P retention in the sediment and its internal processes in aquatic ecosystems make P a key factor that causes eutrophication. In particular, the continued release of legacy P stored in sediments makes it difficult to reduced eutrophication of lakes simple by reducing its input (Jeppesen et al., 2005; Fink et al., 2018; Chorus et al., 2020). The anthropogenic altered nutrient cycles have led to substantial increases in waste accumulation of N and P in aquatic ecosystems (Figure 1.1).

1.1.1.2 Nutrient control in aquatic ecosystems

Reducing nutrient loading is regarded as the fundamental approach to eliminate eutrophication and harmful algal blooms (Moss, 1990; Jeppesen et al., 2005b; Heisler et al., 2008; Conley et al., 2009). The necessary conditions for phytoplankton growth are light, nutrient and temperature. The light and temperature conditions depend on physical and geographical processes of the earth, which are not susceptible to management. Hence, nutrient loading reduction, as the main controllable factor, is needed to combat phytoplankton growth (Heisler et al., 2008) and has been applied to mitigate eutrophication in many countries (Greening et al., 2006; Liu et al., 2007; Gao et al., 2010; Paerl et al., 2016a). However, measures of nutrient loading reduction can be in conflict with the economic development goals of the ambient area (Gren et al., 2008; Zhang et al., 2010). To control the external loadings to aquatic ecosystems, the regulation of the maximum load from ambient domestic, agricultural and industrial discharge is required (Gren et al., 2008; Wang et al., 2019; Tong et al., 2020). For example, in the city Wuxi, China, where a famous eutrophic lake Taihu is located, factories need to be relocated from proximity to the lake to other places to reduce the industrial nutrient discharge, which can result in serious loss of economic income of local residents (Zhang et al., 2010). The construction of wastewater treatment plants is another way to mitigate the nutrient input before the polluted water flows into aquatic ecosystems (Tong et al., 2020). The cost of the construction of wastewater treatment plants is expensive and the experts who can sustain the regular running of the plant require both economic and labour cost (Hu et al., 2010). Similarly, maintenance of wetlands in the vicinity of water bodies for nutrient retention can reduce nutrient loading to aquatic ecosystems (Healy et al., 2002; Gren et al., 2008).

The conservation of such areas is also costly because these areas cannot be used for agricultural activities and generate local income (Libby, 1994). Sediment dredging can be applied to remove the internal loading but it is expensive due to the high cost of the equipment and the variable sediment types (Wates et al., 2016). These economic costs lead to the decision-making and to taking measures of nutrient loading reduction especially difficult (Dong et al., 2015). Since all measures are costly, a feasible and convincing estimation of how much nutrient needs to be reduced is essential for water quality management, so that only the minimum necessary cost needs to be made.

1.1.1.3 Complexity of aquatic ecosystems

The determination of nutrient limits, or in other words thresholds, is essential to aquatic ecosystem management (Kelly et al., 2015). Aquatic ecosystems have the potential to be resistant to nutrient reduction and maintain their current ecological state (Scheffer et al., 2001; Jeppesen et al., 2007a). The theory of alternative stable states in shallow lake ecosystems explains this phenomenon (Scheffer et al., 1993; Scheffer et al., 2001). Shallow lakes usually have two stable states, one is the clear macrophyte-dominated state and another is the turbid phytoplankton-dominated state (Scheffer et al., 1998). A macrophyte-dominated state is often regarded as a healthy ecological state that provides multiple ecological functions and ecosystem services (Costanza et al., 1999), whereas a phytoplankton-dominated state is often a deteriorated ecological state that lacks biodiversity and ecological functions (Hilt et al., 2017). Both phytoplankton and macrophytes are able to maintain their favourable environmental conditions of light and nutrients so that they can sustain the stability of their dominating state (Scheffer et al., 1993). The responses to gradual external perturbations in such lake ecosystems with alternative states are often nonlinear due to their abilities of self-maintenance. The ecological state shift of these ecosystems from one state to another can be sudden.

Once the thresholds are determined, that knowledge can be applied in two ways. Firstly, knowledge of the nutrient threshold supports the restoration of aquatic ecosystems by setting a restoration goal. The restoration goals are especially needed for ecosystems where the global N and P fluxes exceed the boundary of the safe operating space for humanity (Steffen et al., 2015). Secondly, knowledge of the nutrient threshold supports ecosystem conservation by defining the maximum stress that the aquatic ecosystem can absorb. The threshold for conservation is essential for sustaining healthy aquatic ecosystems and to prevent eutrophication (Suding et al., 2009). The nutrient thresholds are often determined based on the load-response curve; i.e., the response of phytoplankton biomass (e.g. represented by chlorophyll-*a*) to a range of nutrient loadings (e.g. P load) (Janse et al., 2008). However, it is challenging to determine these curves because of the complexity of aquatic ecosystems with respect to biogeochemical processes such as food-web interactions, nutrient cycling, hydrodynamics, and the impacts of seasonality including light and temperature (Scheffer et al., 2007). The variability of all these processes or environmental conditions can result in different shapes of load-response curves (Janssen et al., 2017). Since this variability can cause complexity beyond human intuitive understanding, modeling approaches that capture this variance can be useful to determine nutrient thresholds in such complex ecosystems (Ten Broeke et al., 2016; Molenaar, 2019).

1.1.2 Current approaches to determine nutrient thresholds for eutrophication management

Different types of models are developed to derive the load-response curve and to provide solutions to policy-makers for eutrophication management (Janssen et al., 2015; Janssen et al., 2019b). These models differ in their capability to make predictions relevant to target research questions (Soetaert et al., 2008; Dietze, 2017). Empirical models, such as the Vollenweider model, are used a simple regression analysis based on data of phytoplankton biomass and nutrient loading to provide support for eutrophication management (Vollenweider, 1968; 1975; Vollenweider, 1982). This is one of the most commonly used eutrophication models that provides a direct and simple tool for water quality managers to determine the water quality criteria (Reynolds, 1992). Many policy-makers have used it for the reports to reveal their current state of water quality and make policies and provide funding according to the results in these reports (Lee et al., 1981; Rast et al., 1983; Munawar et al., 2011; Chang et al., 2019a). Empirical models such as the Vollenweider model are good tools for estimation of the trophic state for water bodies, but they are limited in their use for scenario analyses of possible futures because they typically miss mechanistic reasoning (Cuddington et al., 2013). Besides, these models are based on calibrated data and thereby are not flexible in their application to ecosystems with different characteristics; e.g. lake size, phytoplankton community, and food web structure that they were initially developed for (Janssen et al., 2019a).

Mechanistic models simulate ecological mechanisms and have the potential to be adjusted to different types of ecosystems (Rastetter et al., 2003). Simple mechanistic models based on ecological theories usually include a limited number of equations. This type of mechanistic model often fits the first principles including a mass balance in ecosystems. For example, Tilman's competition model (Tilman, 1982) can simulate population dynamics of species competition well in chemostat experiments and has been extended to explain biodiversity in the field (Tilman, 1994). Huisman's light competition model (Huisman et al., 1994) can accurately predict which species win in the competition under certain light and nutrient conditions (Passarge et al., 2006) and has been applied in explaining cyanobacterial dominance (Huisman et al., 2004). These types of models are widely applied to explain ecological theories such as species competition (Sommer, 1986; Huisman et al., 2004) and biodiversity (Tilman, 1994; Huisman et al., 1999) but have hardly been applied in aquatic ecosystem management because of the lack of ability to deal with the complex processes in the ecosystem level.

Another type of mechanistic model is the complex process-based models that can perform simulations at the ecosystem level (Janse et al., 1995; Los, 2009; Hipsey et al., 2014). This type of model provides enough details to test scenarios based on specific lake characteristics and variability. For example, the lake ecosystem model PCLake was developed to simulate food web interactions between phytoplankton, zooplankton, and fishes; species competition within phytoplankton functional groups and with macrophytes; nutrient cycling among water column and sediment; and geographical conditions such as lake size and seasonality including light and temperature (Janse, 2005). Such models can be used to test the impact of different scenarios on target ecosystems (Janse et al., 1995) such as the impact of climate change (Mooij et al., 2007), and the nutrient thresholds in terms of the alternative stable states on a local scale (Janse et al., 2008). These process-based models can be questioned, however, when essential processes are not accounted for (Janssen et al., 2015). Besides, uncertainties underlying a large number of parameters and initial conditions may lead to unacceptable predictions (Rowe, 1994).

1.2 Knowledge gap and research aim

A good balance between the pros and cons of current modelling approaches is required to construct models that can determine nutrient thresholds and support eutrophication management towards a sustainable Anthropocene. For a modelling approach, the calibration can only be achieved by data from the past rather than the future. Therefore, future prediction only makes sense when structural changes are considered. One example of a prediction that fails to take into account structural changes can be traced to the Malthus population theory (Malthus et al., 1992, first edition of 1798). His prediction of the human population limit is defined by the hypothesis that human population growth is exponential while food production growth is linear so that the population growth will be limited by resources at the end. However, the prediction based on this hypothesis overlooked the technological advances that allow human beings to extract and consume resources satisfying the demands of population growth (Sachs, 2008). Missing this process in the predictions has led to a conservative prediction for the human population limits and the current population has largely crossed the threshold from his prediction (Van Den Bergh et al., 2004; Tepper, 2015). In other words, when the structural changes due to technological development are considered, the population limit can be seen to actually be dynamic (Ehrlich et al., 1997). Similarly, for the determination of nutrient thresholds, aquatic ecosystems are experiencing climate changes and rising anthropogenic activities. All of these factors can lead to dynamic values of nutrient thresholds (Mayer et al., 2004). Therefore, the determination of nutrient thresholds can only be reached when ecological mechanisms are accounted for (Hilt et al., 2017).

The fundamental mechanism that builds the relationship between phytoplankton and nutrients, i.e. the load-response curve, is essentially based on consumer-resource interactions. Consumer-resource interactions can be defined as processes of how phytoplankton takes up nutrients from the water (Murdoch et al., 1998). Other ecological processes can add details of the consumer-resource interactions to specify the variability of how quick and how much the phytoplankton uptake the nutrients. For example, how the environmental conditions such as light and temperature influence the phytoplankton growth rate (Moore et al., 1995), or how phytoplankton stoichiometry change according to ambient nutrient concentration (Droop, 1974; Klausmeier et al., 2008). Currently, the mechanism of consumer-resource interactions has been established by several seminal mechanistic models (Janssen et al., 2015). For example, Lotka (Lotka, 1925) and Volterra (Volterra, 1928) came up with one of the most classic and pervasive models that abstractly describe the relationship of species growth and environmental capacity and thereby simulates species population dynamics. Later, Tilman (1982) constructed the resource-competition model that provides explicit consumer-resource interactions and has been well validated by experiments from the laboratory (Rothhaupt, 1996; Burson et al., 2018) and field (Wilson et al., 1995; Cahill et al., 2000).

The main question that remains unaddressed, however, is *how the consumer-resource interactions can be used to derive nutrient thresholds and help nutrient management towards a sustainable Anthropocene?* This question gives rise to a number of sub-questions:

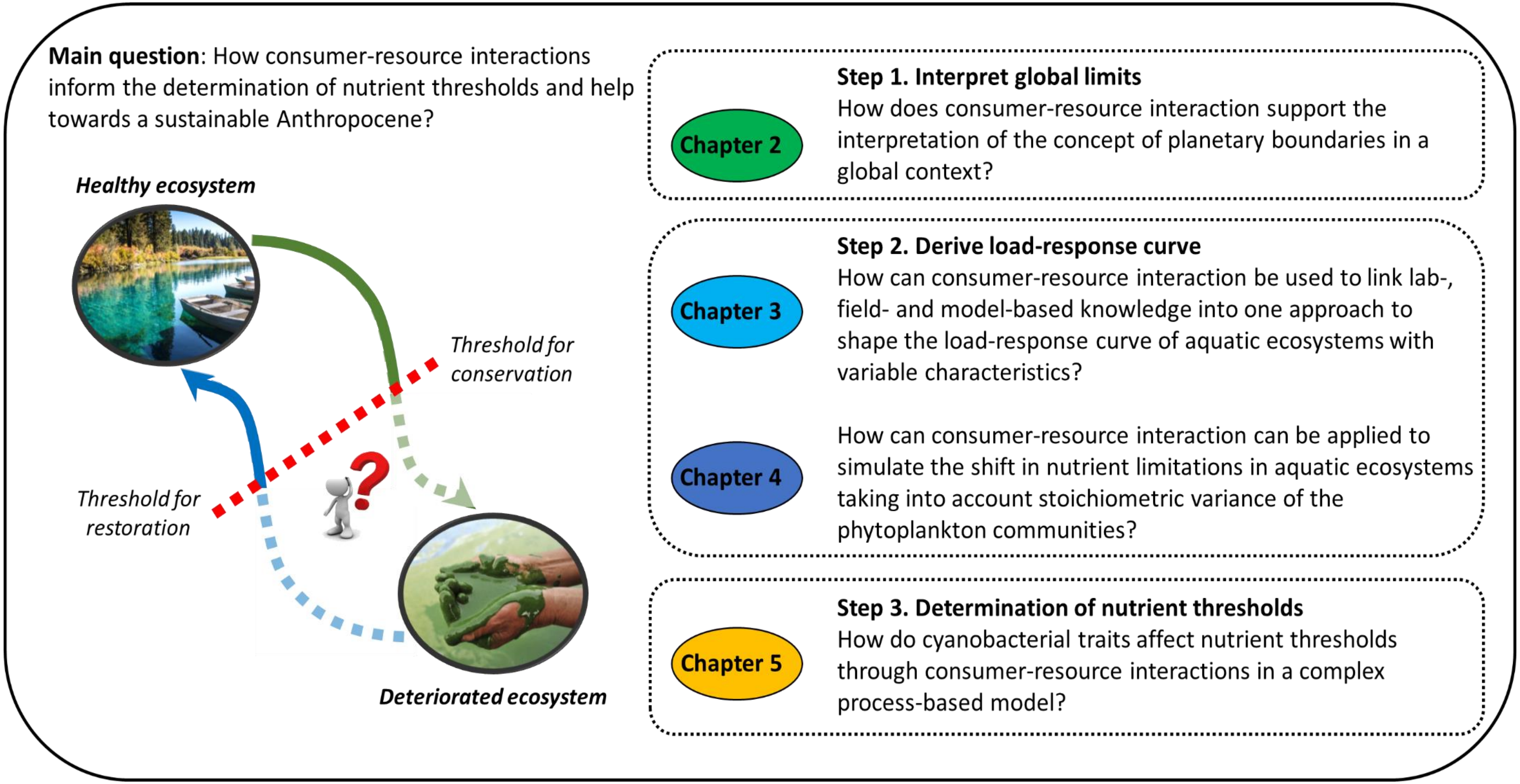
- *how does consumer-resource interaction support the interpretation of the concept of Planetary Boundaries in a global context?*
- *how can consumer-resource interaction be used to link lab-, field- and model-based knowledge into one approach to shape the load-response curve of aquatic ecosystems with variable characteristics?*
- *how can consumer-resource interaction can be applied to simulate the shift in nutrient limitations in aquatic ecosystems taking into account stoichiometric variance of the phytoplankton communities?*
- *How do cyanobacterial traits affect nutrient thresholds through consumer-resource interactions in a complex process-based model?*

1.3 Thesis outline

To answer the research questions, I will make 3 steps (Figure 1.2), starting from interpreting global limits, then deriving the load-response curves and finally determining nutrient thresholds. Four chapters are presented in this thesis to answer the questions raised in section 1.2.

In the first step, I used three models based on consumer-resource theory to interpret the concept of Planetary Boundaries as the global limits (chapter 2). These models include two seminal consumer-resource models, including the Verhulst model of logistic growth (Verhulst, 1845) and Tilman's resource competition model (Tilman, 1982), and one newly developed Resource-Producer-Consumer-Waste (RPCW) model. The purpose in using these models is didactic. The Verhulst model framed the limits as the maximum population of the consumers that can be supported by a certain amount of resource, also referred to as the carrying capacity (Verhulst, 1845). Tilman's resource competition model, on the other hand, showed the limit of the minimum level of resource that consumers can survive. These two models provide the basic concept of the limit for nutrient stress posed by human society, but they need to be interpreted contextually depending on societal processes. One step further, the RPCW model includes the element of waste into the consumer-resource interactions, which is a key need in the current time, in which an excess of waste is the main challenge. In this chapter, the consumer-resource models provide inspirational messages of the realization of the challenges in the Anthropocene.

In the second step, I derived models based on consumer-resource interactions to provide proper load-response curves as tools for eutrophication management in two perspectives (chapter 3 and chapter 4). Firstly, a Generically Parameterized model of lake eutrophication (GPLake) was developed to link the knowledge from the field, lab and modelling studies (chapter 3). The model framework was derived from the differential equations formulated according to the competition theory of light and nutrients (Huisman et al., 1994; 1995). I calculated the relations of the nutrient loading input and phytoplankton biomass at equilibrium and used it as the mechanistic framework of the load-response curve. Based on this mechanistic framework, two generic parameters were defined and calibrated by the data from the field, lab and model studies. These two parameters are formulated by the assemblage of the biological or physical parameters in the original model so that their values can be scaled by lake characteristics such as lake depth and residence time. GPLake can be used as a tool for policy-makers to have a first-order estimation on the trophic state of lake ecosystems. With this first-order estimation, lake managers can easily assess measures such as reducing nutrient load, decreasing residence time or changing depth before spending money on the field-, lab- or model- experiments to support lake management.



Main question: How consumer-resource interactions inform the determination of nutrient thresholds and help towards a sustainable Anthropocene?

Step 1. Interpret global limits
How does consumer-resource interaction support the interpretation of the concept of planetary boundaries in a global context?

Step 2. Derive load-response curve
How can consumer-resource interaction be used to link lab-, field- and model-based knowledge into one approach to shape the load-response curve of aquatic ecosystems with variable characteristics?

How can consumer-resource interaction can be applied to simulate the shift in nutrient limitations in aquatic ecosystems taking into account stoichiometric variance of the phytoplankton communities?

Step 3. Determination of nutrient thresholds
How do cyanobacterial traits affect nutrient thresholds through consumer-resource interactions in a complex process-based model?

Figure 1.2 An overview of the studies presented in this thesis.

One step further, a stoichiometric extension of GPLake model was developed and named as GPLake-S (chapter 4). This is a model that defines the relationship of both N and P loading as nutrients input and the phytoplankton biomass represented as chlorophyll-*a.* GPLake-S accounts for variable stoichiometry of the phytoplankton community under different nutrient N:P ratios, hence leading to different load-response curves. In this chapter, I calculated the relations of nutrient input and phytoplankton biomass based on resource competition theory from two to multiple species competing for two essential resources N and P. Due to the focus on the relations of nutrient input and phytoplankton biomass, I compared the results of the total phytoplankton biomass from the species competition with a series of the nutrient loadings with different ratios and amounts. I found that under reasonable assumptions, the simulation with three species captures 97% of the results of phytoplankton biomass that would be attained if there were a large number of species. Therefore, I decided to formulate the GPLake-S model with three representative species: two species that represent the most extreme species under P-limited (α) and N-limited (β) conditions and an intermediate species (μ) which represent the species present under the co-limitation of N and P. GPLake-S was parameterized by the data from lab, field and modelling studies. Finally, I achieved a model with five planes including the N-limited plane, P-limited plane, two co-limited planes and one light-limited plane. Specifically, this model can help with identifying the limits of both N and P loadings that can provide estimations of the chlorophyll-*a* level and the limiting factors, including N, P ecosystem management.

In the third step, I explored how the competitive traits of harmful algal species cyanobacteria can affect consumer-resource interactions in specific lake ecosystems and alter the nutrient threshold, which is defined as nutrient loading threshold (chapter 5). An established process-based model PCLake+ was extended by adding new ecological processes related to cyanobacterial traits, including buoyancy regulation and nitrogen fixation. By using this model, nutrient loading thresholds at which the lake ecosystem will shift from a clear macrophyte-dominated state to a turbid phytoplankton-dominated state or the reverse, can be obtained. To explore the impacts of cyanobacterial traits, I obtained nutrient loading thresholds by performing four scenarios, including cyanobacteria without traits, with buoyancy regulation, with nitrogen fixation, and with both traits. Besides the nutrient loading thresholds, PCLake+ is able to provide information about ecological mechanisms, such as how cyanobacterial traits influence the nutrient limitation and light limitation to cyanobacteria. This information increases the understanding of the mechanisms for ecological feedback that affect the resilience of the lake ecosystem and result in the changes of nutrient loading threshold values. This model provides a tool that is able to be adjusted for specific lake ecosystems and to test more scenarios in future studies.

Chapter 2

Learning from generations of sustainability concepts

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Abstract

Background: For decades, scientists have attempted to provide a sustainable development framework that integrates goals of environmental protection and human development. The Planetary Boundaries concept (PBc) – a framework to guide sustainable development – juxtaposes a 'safe operating space for humanity' and 'planetary boundaries', to achieve a goal that decades of research have yet to meet. We here investigate if PBc is sufficiently different to previous sustainability concepts to have the intended impact, and map how future sustainability concept developments might make a difference.

Design: We build a genealogy of the research that is cited in and informs PBc. We analyse this genealogy with the support of two seminal and a new consumer-resource models, that provide simple and analytically tractable analogies to human-environment relationships. These models bring together environmental limits, minimum requirements for populations and relationships between resource-limited and waste-limited environments.

Results: PBc is based on coherent knowledge about sustainability that has been in place in scientific and policy contexts since the 1980s. PBc represents the ultimate framing of limits to the use of the environment, as limits not to single resources, but to Holocene-like Earth system dynamics. Though seldom emphasized, the crux of the limits to sustainable environmental dynamics lies in waste (mis-)management, which sets where boundary values might be. Minimum requirements for populations are under-defined: it is the *distribution* of resources, opportunities and waste that shape what is a safe space and for whom.

Discussion: We suggest that PBc is not different or innovative enough to break 'Cassandra's dilemma' and ensure scientific research effectively guides humanity towards sustainable development. For this, key issues of equality must be addressed, un-sustainability must be framed as a problem of today, rather than projected into the future, and scientific foundations of frameworks such as PBc must be broadened and diversified.

'The environment does not exist as a sphere separate from human actions, ambitions, and needs, and attempts to defend it in isolation from human concerns have given the very word 'environment' a connotation of naivety in some political circles. The word 'development' has also been narrowed by some into a very limited focus, along the lines of 'what poor nations should do to become richer', and thus again is automatically dismissed by many in the international arena as being a concern of specialists, of those involved in questions of 'development assistance'.' Gro Brundtland (Brundtland Commission, 1987).

2.1 Introduction

Over the last decade, the Planetary Boundaries concept (PBc) (Rockström et al., 2009a; Rockström et al., 2009b) has been highly cited in academic contexts (Downing *et al* 2019); it has been widely applied as a framework for sustainable business and sustainability campaigning (e.g. https://houdinisportswear.com/en-se/sustainability/planetary-boundaries-assessment; https://www.weforum.org/agenda/2015/01/9-ways-to-pull-our-planet-back-from-the-brink/; https://www.loreal.com/sharing-beauty-with-all-living/assessing-the-footprint-of-our-products/a-new-tool-to-assess-the-environmental-and-social-impact-of-our-products); frequently raised in policy forums (Galaz et al., 2012)– and also sometimes strongly contested (Montoya et al., 2018; Rockström et al., 2018). We view the framing of 'boundaries' in PBc as a vital part of the reason for the impact of the concept.

The limits (or boundaries) presented in the PBc separate an environmental 'danger zone' – where thresholds to Earth system dynamics are likely to exist – from a Safe Operating Space (SOS) for humanity. The SOS represents Holocene-like Earth system dynamics, where Earth system processes continue to function as they have over the past ±12 thousand years while human societies have developed and thrived to become the dominant shapers of Earth system change (Rockström et al., 2009b; Steffen et al., 2015). In bringing together both Planetary Boundaries and a Safe Operating Space for humanity, the PBc brings to culmination centuries of work on the dependencies of societies on their environment, that has often been framed as a duality of nature protection goals in contrast to human development goals.

Greek mythology tells the story of a princess of Troy – Cassandra – who was gifted with prophecy but cursed that she would not be believed. Though she warned of the invasion and fall of Troy, she could not prevent it, and may have been blamed for it. In a similar way, centuries of research that carry a seemingly consistent message: 'human impacts outpace the natural environment's ability to support humanity' have yet to yield necessary changes (Oreskes, 2014).

The first intergovernmental "Biosphere Conference" held in Paris in 1968 marked a shift in international perspectives on development (Unesco, 1968). Here, the word 'Biosphere' appeared on the world stage and was anchored into everyday language. Humans, including their social interactions, were recognized as an integrated part of the biosphere, and a key factor in modifying the biosphere. The conference's most marking output was the recognition that environmental protection and human development go hand in hand. This message was repeated in the United Nations conference on the Human Environment in Stockholm (United Nations, 1972a; b); and the Brundtland report (1987). Forty years on, the publication of PBc indicates that the goals of these conferences are still far off.

In this article, we ask if PBc has what is needed to break Cassandra´s dilemma. We seek to identify how PBc differs from existing sustainability frameworks and research and what novel perspectives it brings. With the aim of better informing the design and implementation of future sustainable development research, we here compile centuries of knowledge on human impacts on their life support system. We highlight path-dependencies of ideas that have informed PBc and point to potential gaps that could be explored in future concept developments.

We first build a 'genealogy' of the literature the Planetary Boundaries article cites as foundations, i.e. literature that is listed in 'the three branches of scientific inquiry' (Rockström et al., 2009b) as well as the body of science upon which these branches rest. We review the science that informs the PBc to understand how the environmental and human components of sustainable development have been brought together, analysing how the PBc builds on and importantly *distinguishes* itself from two centuries of research on the perceptions of the limited capacity of the environment to support societies (since Malthus, 1798).

We support this analysis with insights from two seminal and a new consumer-resource models. Our purpose in using these models is didactic. They are an illustration of the overarching duality between conservation and poverty alleviation perspectives. Furthermore, they highlight interdependencies between aims of 'conservation' and 'poverty alleviation' and thus suggest a new perspective from which to build future integrated social-ecological sustainability concepts. Indeed, these models are part of the basis of the research on which the PBc is built (e.g. Lotka, 1925) and they provide a caricatural yet analytically tractable analogy to human-environment relationships. In seminal consumer-resource models, limits are typically framed in two ways (see Box 2.1 for details): either as the maximum population size a resource base can support - often referred to as the carrying capacity (K) (Verhulst, 1845), or as the minimum amount of resources consumers need to survive and produce a next viable generation - often referred to as Tilman's R^* (Tilman, 1982). This minimum amount of resource captures a key component of the Malthusian catastrophe (1798) which postulates that ultimately human population size will be limited by famine.

Box 2.1 Two seminal consumer-resource models

Logistic growth of the human population sensu Verhulst

The mathematician and demographer Verhulst (1845) was the first to explicitly model the limits to human population size with what he called the logistic curve:

$$\frac{dC}{dt} = r_{Cmax} C \left(1 - \frac{C}{K}\right) \Rightarrow C^* = K$$

where C is number of humans (population unit), r_{Cmax} is maximum per capita birth rate (rate unit), C^* is maximum number of humans that can be sustained (population unit), which is equal to carrying capacity K (population unit). The model describes the shift from a positive feedback of population size on itself at low numbers towards a negative feedback of population size on itself at high numbers. Whereas the positive feedback at low numbers leads to an initial exponential growth phase, the negative feedback at high numbers makes population size settle at carrying capacity.

Human population size constrained by resource scarcity sensu Malthus

The strength of the logistic growth model is that it provides the limitations to population growth in its most condensed form. However, being a heuristic model, it provides little insight into the mechanisms through which the negative feedback happens. For this we need an explicit consumer-resource model (Tilman 1982):

$$\frac{dR}{dt} = r_R R_{res} - l_R R - r_C q_{R\to C} C$$

$$\frac{dC}{dt} = r_C C - l_C C$$

with

$$r_C = r_{Cmax} \frac{R}{R + H_R}.$$

This model has two dynamically modelled state variables and seven parameters. R represents the available resources (resource unit); C the number of consumers (population unit); R_{res} the reserve from which resources are made available to consumers (resource unit); r_R the proportional rate at which resources are made available to consumers from the reserve (rate unit); l_R the background rate at which the available resources are lost without being consumed (rate unit); $q_{R\to C}$ the conversion from available resources to consumers (resource unit/population unit); r_{Cmax} the maximum per capita birth rate of consumers (rate unit); H_R the resource availability at which the realized per capita birth rate of consumers equals half of their maximum per capita birth rate (resource unit) and l_C the per capita mortality rate of consumers (rate unit). The auxiliary variable r_C represents the realized per capita birth rate of consumers as function of resource availability.

Box 2.1 (Continued.)

The model has two equilibria that we named a 'pristine world' (PRW) – in which resource density (R^*_{PRW}) is controlled by other processes than consumption and consumers (C^*_{PRW}) cannot exist or have not yet invaded the system:

$$R^*_{PRW} = \frac{r_R}{l_R} R_{res}$$

$$C^*_{PRW} = 0$$

and a 'resource limited world' (RLW) in which the sustainable number of consumers C^*_{RLW} is limited by the resource availability R^*_{RLW}:

$$R^*_{RLW} = \frac{H_R l_C}{r_{Cmax} - l_C}$$

$$C^*_{RLW} = K = \frac{r_R R_{res} - l_R R^*}{l_C q_{R \to C}}$$

One of the major outcomes of this model is that when the consumer population has reached its maximum sustainable size at carrying capacity $K = C^*_{RLW}$, the resource availability is reduced to a critical low value R^*_{RLW} that allows individual consumers to produce offspring at replacement level. Remarkably, this minimal resource availability R^*_{RLW} is not dependent on the size of the resource reserve R_{res} from which resources are extracted or the rate at which this happens r_R. Together, these findings seem to capture the essence of the Malthusian catastrophe (1798) that irrespective of any conceivable advancement in agricultural production, consumer population growth will always be able to catch up until the resources are again depleted to the same level as before and starvation once more limits offspring to replacement level. We can generalize the advancement in agricultural production on which Malthus focused to any technological innovation in society that increases its access to resources. Sensu Tilman (1982), the model can be expanded to capture the competition between individual consumers, or groups of consumers, that differ in their ability to acquire resources, i.e. the topic of inequality.

Whereas the seminal consumer-resource models of Box 2.1 capture the population dynamics of many organisms, its Malthusian assumption that scarcity in resources directly translates into increased consumer mortality is unrealistic in the context of contemporary societies. Moreover, when we started applying the K-R^* analysis to each of the PBc's nine Earth system processes, we noted that at least six of the nine Planetary Boundaries relate to processes of waste accumulation rather than resource limitation (Table 2.1). For these reasons, we interpreted the PBc in terms of a new Resource-Producer-Consumer-Waste (*RPCW*) model. Acknowledging that in modern societies, resource acquisition and limitation is driven by economics, we make a distinction between the production and consumption of resources and move from expressing consumers in terms of numbers into expressing them in terms of the resource they possess (Box 2.2). Moreover, the new model captures the deleterious impacts of waste accumulation on human consumption. We use the analogies with the seminal and the new consumer-resource models to analyse the evolution of limits in the concepts on which the PBc is built.

2.2 Methods

2.2.1 Genealogy of literature

We first create a genealogy of the literature on which the Planetary Boundaries is built by selecting the work cited in Rockström et al., 2009a as the three *'branches of inquiry'*. These branches of inquiry are: (a) the scale of human action in relation to the capacity of the Earth to sustain it; (b) understanding essential Earth System processes and (c) framing of resilience (see Appendix 2.1, Table A2.1). From these 22 direct references, we use a 'snowball' approach to identify secondary sources. In each direct reference, we select the sources to the core ideas being developed (Figure 2.1). For example, Bretherton (NASA Advisory Council 1986, National Research Council 1988) cite Newton, Hutton, Lyell and Darwin as the founders of the Earth system science that is built upon. Similarly, Holling (1973) builds on analyses of diversity and stability by May (1971), Lewontin (1969) and MacArthur (1955) (*inter alia*). We do not select all possible secondary references, but we build a comprehensive library of 58 direct and secondary references. Finally, we analyse the relationship between these references, in a systematic 'who-cites-who' approach (see Table A2.1). Unfortunately, not all older secondary references were directly searchable. Also, we here emphasize that the approach is not sufficient for a quantitative or systematic analysis of the network of references, since the referencing method and style of individual authors, types of publications (journals, reports or books) are very different and somewhat arbitrary (Borgman, 2015). Furthermore, some concepts and ideas are often not (or mis-) attributed (e.g. the concepts of carrying capacity or cybernetics for instance), and a search for references can be murkied when an author name is common (e.g. Thomas), confusable (e.g. E. P. Odum, vs. H. T. Odum) or a common verb or noun (e.g. May and Marsh).

2.2.2 Consumer-resource models

Here we present a new Resource-Producer-Consumer-Waste *(RPCW)* model that deals with the shortcomings of the seminal consumer-resource models (see Box 2.1 for details on these models) to illustrate some dynamical aspects of the Planetary Boundaries. The model identifies four pools of resources of which three are modelled dynamically. In the model resources (R) are used by producers (P) to make goods for consumers (C) who then turn these goods through usage into waste (W). For example, oil may be extracted from an underground resource reserve R_{res} and after refinery become part of the stocks held by producers P. From there it will enter the stocks held by consumers C through retail and finally be emitted to the atmosphere as waste W through combustion. To keep the model as simple as possible we defined each state variable in the same unit so that we can leave out conversion factors between resources in the reservoir, held by producers and consumers and in the waste compartment. For the oil example this would imply that all pools would be expressed in masses of carbon. For details on the *RPCW* model see Box 2.2.

Box 2.2 A new Resource-Producer-Consumer-Waste model

The aim of the newly developed Resource-Producer-Consumer-Waste (RPCW) model is to add waste limitation to the resource limitation that is key to the seminal *consumer*-resource model described in Box 1. Moreover, instead of modelling the number of consumers, we now model the amount of resources they have in their possession thereby keeping the unit of all state variables in the model the same. Finally, we acknowledge that in human society resources are not taken up directly from the environment but rather acquired from producers who themselves obtain these resources from the environment. We used the following color codes to link the RPCW model with the 'three branches of scientific inquiry' underlying the PBc. Terms that describe how producers and consumers interact with the Earth system are marked blue. Interactions among producers and consumers are marked purple and those terms in the model that make it nonlinear are marked orange:

$$\frac{dP}{dt} = r_P R_{res} - l_P P - r_C C$$

$$\frac{dC}{dt} = r_C C - l_C C$$

$$\frac{dW}{dt} = l_C C - l_W W$$

$$r_C = r_{Cmax} min\left(\frac{P}{P + H_P}, \frac{{H_W}^b}{W^b + {H_W}^b}\right)$$

The model has three dynamics state variables and nine parameters. We decided not to model the resource reserve dynamically, but rather keep this state at a constant level R_{res} to keep the model simple and avoid the need to make a distinction between renewable and non-renewable resources. In the model P is the pool of resources made available by producers to consumers, C is the pool of resources acquired by consumers, W is the pool of resources turned into waste by consumers, r_C is the realized rate at which consumers acquire resources (rate unit), R_{res} is the reserve from which producers extract resources to make them available to consumers, r_P is the rate at which producers extract resources from the reserve (rate unit), l_P is the loss rate of unsold extracted resources (rate unit), r_{Cmax} is the maximum rate at which consumers acquire resources if they were not limited (rate unit), l_C is the realized rate at which consumers turn acquired resources into waste through usage (rate unit), H_P is the level of resources offered by producers to consumers at which the realized rate of acquisition of resources by consumers is half the maximum rate of acquisition (resource unit), H_W is the level of waste experienced by consumers at which the realized rate of acquisition of resources by consumers is half the maximum rate of acquisition (resource unit), b is the shape parameter of the waste limitation function for consumers (unitless) and l_W is the rate at which waste is lost through natural decay or active waste treatment (rate unit).

Box 2.2 (Continued.)

The *RPCW*-model has three sets of equilibria. We named the first set a 'pristine world' (PRW) in which there are only resources and no consumers, the second set a 'resource limited world' (RLW) in which the acquisition of resources by consumer is limited by resource scarcity, and the third set a 'waste limited world' (WLW) in which the acquisition of resources by consumers is limited by waste accumulation as follows:

Equilibria	Pristine World (PRW)	Resource Limited World (RLW)	Waste Limited World (WLW)
P^*	$\frac{r_P}{l_P} R_{res}$	$\frac{l_C}{r_{Cmax} - l_C} H_P$	$\frac{r_P}{l_P} R_{res} - \frac{l_W}{l_P} W^*_{WLW}$
C^*	0	$\frac{r_P}{l_C} R_{res} - \frac{l_P}{l_C} P^*_{RLW}$	$\frac{l_W}{l_C} W^*_{WLW}$
W^*	0	$\frac{l_C}{l_W} C^*_{RLW}$	$\left(\frac{r_{Cmax} - l_C}{l_C}\right)^{\frac{1}{b}} H_W$

We studied the impact of changing each of the model parameters on the values of the equilibria. These bifurcation analyses also show how changing the parameters can induce switches between the pristine, the resource limited and the waste limited world and at which critical parameter values this happens. (See Appendix 2.2 for detailed output of these analyses.) Here we give an overview of the general patterns that we found:

Parameter value*	Pristine World (PRW)			Resource Limited World (RLW)			Waste Limited World (WLW)			Parameter value*
	P^*	C^*	W^*	P^*	C^*	W^*	P^*	C^*	W^*	
r_P R_{res} l_P	↗	0		=	↗		↗	=		r_P R_{res} l_P
l_W	NA			=		↗	↗	↘	=	l_W
r_{Cmax} l_C	=	0		↘	↗		↘	↗		r_{Cmax} l_C
H_P	NA						=			H_P
H_W b				=			↗	↘		H_W b

Box 2.2 (Continued.)

For each of the nine parameters of the model we specify the impact of changing that parameter on the equilibrium amount of resource held by producers (P^*), held by consumers (C^*) and in the waste compartment (W^*) goes up (arrow upwards), stays equal (=), goes down (arrow down), equals zero (0) or cannot exist (NA) in the pristine world, the resource limited world and the waste limited world. The font size of the parameters on either side of the table shows whether we increased (e.g from $\scriptstyle r_P$ to r_P) or decreased (e.g. from l_P to $\scriptstyle l_P$) a given parameter to move from the pristine through the resource limited to the waste limited world.

The main findings of this analysis can be summarized as follows. With increasing the values of r_P, R_{res}, r_{Cmax} and b (± increased access to resources) and with decreasing the value of l_P, l_W, l_C, H_P and H_W we move from the pristine world through the resource limited world to the waste limited world. Within the resource limited world, consumers can increase the amount of resources they possess by increasing r_P, R_{res} and r_{Cmax} or by decreasing l_P, l_C or H_P with the other parameters having no effect. Within the waste limited world, consumers can increase the amount of resources they possess by increasing l_W, r_{Cmax} or H_W or by decreasing l_C or b with the other parameters having no effect. The main message is when technological development only focusses on making resource more available (i.e. increasing r_P and R_{res} while decreasing l_P) we necessarily end up in the waste limited world, as seems indeed the case with six of the nine Planetary Boundaries being caused by waste accumulation (Table 1). The best options to find a balance between a resource limited and a waste limited world are by technological advancement in the waste treatment rate (i.e. increasing l_W) or reducing the realized consumption rate (i.e. decreasing l_C).

2.3 Results

2.3.1 The scale of human action in relation to the capacity of the Earth system to sustain it

An overarching thematic of this branch of inquiry lies in the closed, finite nature of the Earth system (Boulding, 1966), and its resources (Costanza, 1991), that builds on von Bertalanffy's (1960) work on steady-states and systems theory (Tables A2.1 & A2.2). The main emphasis of this branch of inquiry rests at sub-global levels, where carrying capacities are understood as dynamic and variable (Odum, 1989; Arrow et al., 1995), and where diverse contexts matter as well as the heterogeneity of distribution of resources and environmental impacts. In this branch of inquiry, the burden of quantification and balancing is on the economic system - as a tool for the management of natural resources – and the environment is valued qualitatively (Arrow *et al* 1995, Costanza 1991). Ecological economics focuses on the rules for the sustainable management of natural resources: non-renewables should be exploited at a rate no higher than the substitution of non-renewable to renewable resources; renewable resources should not be extracted at a rate higher than the rate at which they renew; and technology should focus on making the use of resources more effective, rather than on making their extraction more effective. Most of the PBc's Earth system processes are addressed, not in the interest of determining their limits, but to determine appropriate accounting for impacts on these processes in the economic systems (e.g. as intergenerational impacts; as costs to those who benefit from making impacts). A strong thematic, reinforced in the framework of the tolerable windows approach, is the capacity for human control of impacts to the environment.

Table 2.1 Interpreting the PBc in terms of the RPCW model. For each boundary we first identify whether it primarily involves resource scarcity (marked in blue) or waste accumulation (marked in orange) and identify the critical resource or waste involved. Moreover, we identify whether the PB is defined in terms of a process or a state. Next we identify the fundamental imbalance that leads to crossing the boundary and the resulting unsustainability in terms of the parameters and states of the RPCW model. Finally we express the solution for not crossing the PB - and hence staying in the Safe Operating Space - in terms of the model parameters. For the PBs caused by waste accumulation this solution lies in reducing consumption (= decrease in l_C) or improving waste treatment (= increase in l_W). For the PBs dealing with resource scarcity in water and topsoil this solution lies in reducing the rate at which producers extract resources from the reserve (= decrease r_P). The solution to PB9 dealing with biodiversity is outside the scope of the RPCW model.

PB#	**Planetary Boundary**	**Primary problem**	**Critical resource/ waste**	**Defined in terms of**	**Fundamental imbalance**	**Resulting unsustai-nability**	**Solution**
PB1	Climate change	Waste accumulation	Greenhouse gasses	Process	$l_C C > l_W W$	Increase in W	Decrease in l_C or increase in l_W
PB2	Novel entities (chemical pollution)	Waste accumulation	Novel entities/ chemical pollutants	State	$l_C C > l_W W$	Increase in W	Decrease in l_C or increase in l_W
PB3	Stratospheric ozone depletion	Waste accumulation	Ozone-depleting substances	Process	$l_C C > l_W W$	Increase in W	Decrease in l_C or increase in l_W
PB4	Atmospheric aerosol loading	Waste accumulation	Fine particles/ droplets	Process	$l_C C > l_W W$	Increase in W	Decrease in l_C or increase in l_W
PB5	Ocean acidification	Waste accumulation	Carbon dioxide	Process	$l_C C > l_W W$	Increase in W	Decrease in l_C or increase in l_W
PB6a	Biochemical flows (nitrogen)	Waste accumulation	Nitrogen	Process	$l_C C > l_W W$	Increase in W	Decrease in l_C or increase in l_W
PB6b	Biochemical flows (phosphorus)	Waste accumulation	Phosphorus	Process	$l_C C > l_W W$	Increase in W	Decrease in l_C or increase in l_W
PB7	Freshwater use	Resource depletion	Water	Process	$r_P R_{res}$ unsustainable	Decrease in R_{res}	Decrease in r_P
PB8	Land system change (loss of topsoil)	Resource depletion	Topsoil	Process	$r_P R_{res}$ unsustainable	Decrease in R_{res}	Decrease in r_P
PB9a	Biosphere integrity (functional diversity)	Resource depletion	Functional diversity	State	R_{res} decreasing	Decrease in R_{res}	Not covered by the model
PB9b	Biosphere integrity (genetic diversity)	Resource depletion	Genetic diversity	State	R_{res} decreasing	Decrease in R_{res}	Not covered by the model

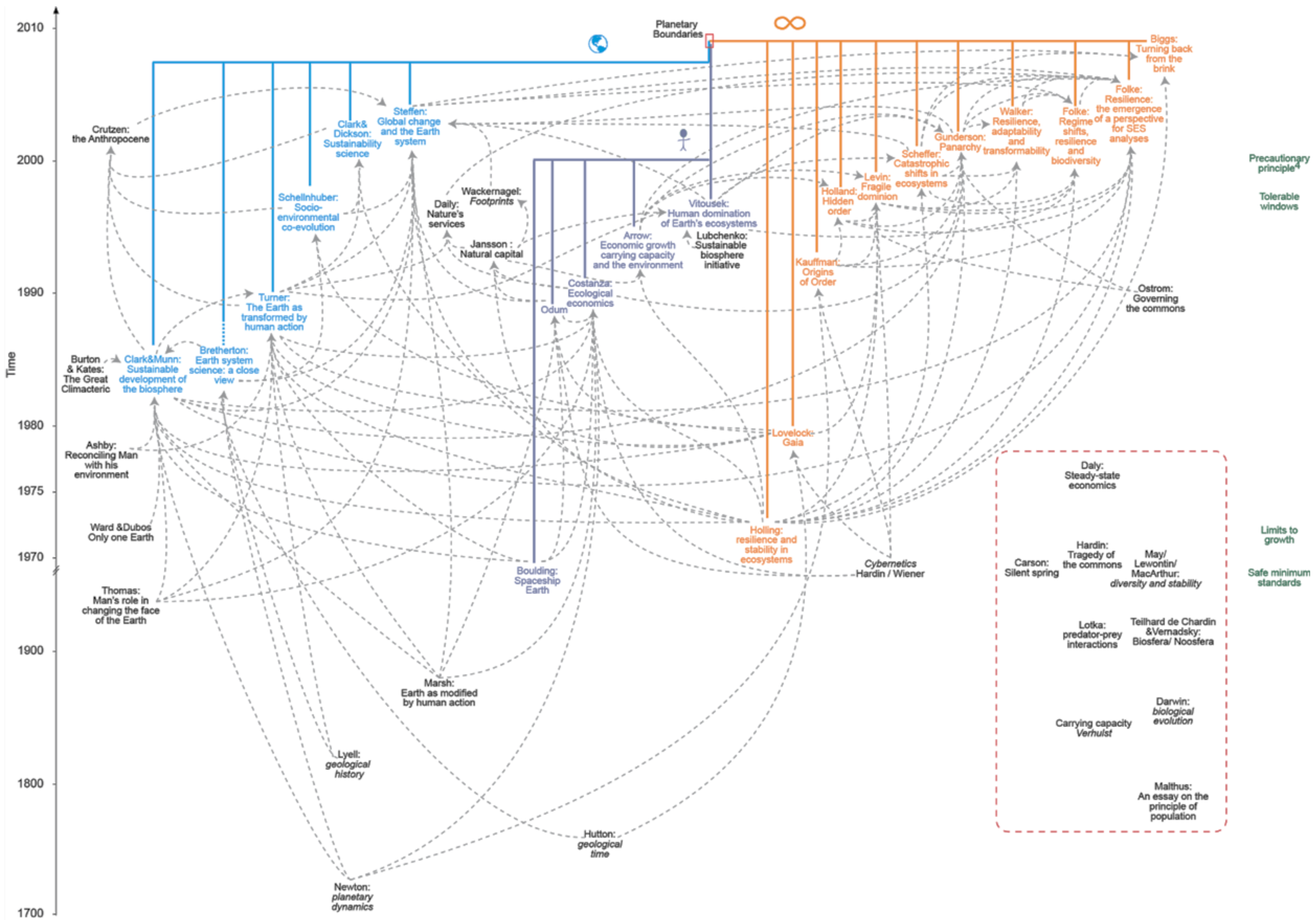

Figure 2.1 The genealogy of Planetary Boundaries science, references are placed according to year of publication. Couloured references represent those directly referenced in Rockström et al (2009b). In blue, the branch of inquiry relating to Earth system processes; in purple, the scale of human action in relation to the capacity of the Earth to sustain it; in orange, the framework of resilience; in green, the frameworks on which the PBc builds. In black are secondary references, i.e. those that shape the science on which the PB is built. For clarity, we have removed lines representing citations between secondary references, and the secondary references that are cited more than 10 times are in red. For the full citation analysis, see Table A2.2. A high resolution of this figure is available online: https://iopscience.iop.org/article/10.1088/1748-9326/ab7766.

2.3.2 Understanding essential Earth system processes

This branch of inquiry focused on understanding Earth system dynamics finds its roots as early as the 17th century, in Newton, then Hutton, Lyell, and Darwin. Turner *et al*'s book '*The Earth as Transformed by Human Action*' (1990) builds from Ashby's '*Reconciling Man with the Environment*' (1978), which in turn builds from Thomas *et al*'s '*Man's Role in Changing the Face of the Earth*' (1956), which itself finds roots in Marsh's '*The Earth as Modified by Human Action*' (1874) (Figure 2.1, Table A2.2).

In this literature, the work of Clark and Munn Clark et al., 1986 has the broadest roots, drawing from economics (e.g. Boulding, 1966, resilience (e.g. Holling, 1973), and Earth system science to discuss not only sustainable levels of impacts, but also anthropological perspectives (e.g. contributions by Timmerman et al., 1986), SIon human perceptions and conceptions of sustainability, and ethics. 'Planet under Pressure' Steffen, 2004 follows on the approach and work of Marsh (1874), Thomas *et al* (1956), Ashby (1978), Turner *et al* (1990), Burton and Kates (1986), Bretherton (NASA Advisory Council 1986, National Research Council 1988) and Clark *et al* (1986). Here the approach is to first understand and describe Earth system dynamics, then how impacts of humanity influence Earth system dynamics and finally, to address the critical questions regarding how Earth system change influences human well-being.

Schellnhuber et al (1998; 1999) take a slightly different approach, focusing on the co-evolving feedbacks between social-ecological systems and the potential breaking points of these feedbacks - Nature and Humanity are more closely integrated. This work builds on the concept of Gaia (Lovelock et al., 1969; Lovelock et al., 1974) and the concept of cybernetics, self-regulation and co-evolution. Geocybernetics (Schellnhuber and Kropp 1998) follows the line of thought of Vernadsky and de Chardin's Noösphere (Teilhard de Chardin, 1955; Vernadsky, 1986; Levit, 2000): where the self-regulating processes expand and evolve, technology and geocybernetics are the next steps of social-ecological co-evolution. Despite these slight differences in perspectives – where the first approach predominantly aims to quantify processes and the cybernetics approach tends towards understanding mechanisms and qualifying changes – the approaches don't contradict each other. Their commonalities are crystallized in the framing of the Anthropocene (Crutzen, 2002), which brings together the co-evolutionary, cybernetic visions of the Biosfera (Vernadsky 1986), Noösphera (de Chardin 1955), Gaia (Lovelock and Giffin 1969), and Geocybernetics (Schellnhuber and Kropp 1998), with the understanding of Earth system dynamics and impacts of Human action thereon (e.g. NASA Advisory Council 1986, National Research Council 1988, Turner *et al* 1990, Clark *et al* 1986). The Earth system branch of inquiry builds towards the global level (see Table A2.2, and as exemplified in Schellnhuber 1999), where the branch of inquiry on human impacts brings out differentiated contexts. Clark et al., 2003 is not about Earth system sciences, but rather about science and technology as both are seen to '*take as their point of departure a widely shared view that the challenge of sustainable development is the reconciliation of society's development goals with the planet's environmental limits*'. The article is in large part a response to global policy events and documents (such as the world summit on sustainable development in 2002, and United Nations (1992, 1987) that call for more research into sustainable development.

2.3.3 Resilience

The resilience and complex systems framing branch of inquiry has a central commonality on feedbacks and systems thinking. Where the Earth system branch looks at what the Earth system processes and elements are, the resilience branch of inquiry investigates how they interact (e.g. Holland, 1995, Kauffman, 1993, Gunderson et al., 2002). The first edition of Gaia (Lovelock and Giffin 1969) assumed self-regulation and homeostasis. In later editions however, Human action is framed as a disruption to self-regulatory, homeostatic processes, and the author thus calls to containing human activities (Lovelock, 1989; Lovelock, 1991). This contrasts with Schellnhuber's framing, where the expansion of human technology and knowledge to respond to human-induced environmental degradation is part of self-regulating processes. Though this difference is subtle – resting on a normative assessment of where limits between self-regulation and deregulation might stand – it also reflects a difference in underlying assumptions. In the same vein as the Noösphere, geocybernetics' socio-environmental co-evolution (Schellnhuber and Kropp 1998) assumes a level of determinism and directionality to evolution that is not present in the later versions of Gaia. Cybernetics and feedback mechanisms are core to the branch of inquiry of Resilience and to the PBc concept, but the assumption of directionality and self-regulation for or towards human well-being is not. In this way, PBc also responds to the perspectives of the intergovernmental Biosphere conference, which cites limits to the 'plasticity' of ecosystems and risks of irreversible changes (Unesco 1968).

The branch of resilience builds on the adaptive cycle (Holling, 1986; Gunderson et al., 2002), focusing on why feedbacks are important for humanity: the risk of catastrophic shifts and irreversible changes (Scheffer et al., 2001; Biggs et al., 2009), and how societies manage or can be trapped in such dynamics (e.g. Walker et al., 2004). Holling's seminal work (1973) permeates across branches of inquiry, specifically the focus on sudden changes in systems, as opposed to gradual changes, and on the notion of stability, as dynamic rather than static (MacArthur, 1955; Lewontin, 1969; May, 1971). Where the Earth science and human impacts branches of inquiry primarily describe impacts to the Earth system, the resilience framing brings in the notion of limits, dynamic, context and scale specific.

The three branches of inquiry, though distinct in field and themes of focus, share much common ground. All are rooted in the central work of Holling (1973) and build a common school of thought. Indeed, many of the authors in the genealogy, e.g. Holling, Odum, Boulding, Clark, Costanza, Schellnhuber and Folke, to name but a few, are co-authors in each other's articles, co-editors of books and contribute chapters in each other's books. Of course, the genealogy is not comprehensive, and key scientists whose broader corpus of work have shaped the thinking behind PBc and its genealogy do not appear explicitly here, such as for example C.S. Elton, E.O. Wilson, A.H. and P.R. Ehrlich and S.R. Carpenter. This stems in part from the fact that in some instances, the critical ideas are related to people and their broad corpus rather than to specific references.

2.3.4 Interpreting the PBc in terms of K and R^*

Already most of the PBc's nine (eleven if the subdivisions in Biosphere Integrity and Biogeochemical Flows are included) Earth system processes were addressed in Meadow's *et al*'s limits to growth (Meadows et al., 1972), and by the Bretherton diagram in 1986, essentially all Earth system processes defined in the PBc had been brought to the fore.

In the genealogy, the early literature relating to Earth system science centres on determining changes in the Earth system's carrying capacity (K), with the underlying assumption or corollary that this interferes with humanity's basic needs. These needs (R^*) however are not specified beyond the need for sustainability (Clark *et al* 1986). In much of this literature, human requirements are basic physiological needs: (clean) water and air, food. Steffen *et al* (2004) incorporate a more systemic nature of needs, i.e. need for a relatively stable and predictable environment, which is core to the PBc's definition of a Safe Operating Space. Throughout this literature, needs are seen as homogeneous, common to the whole of humanity, though Steffen *et al* (2004) cite the heterogeneous distribution of vulnerability.

The literature on the scale of human action is built on three sublines of inquiry (Rockström *et al* 2009a, see Table A2.1). Ecological economics (Costanza, 1991) and Biophysical constraints to the economic system (Boulding, 1966; Daly, 1991; Arrow et al., 1995), are sublines that look not at humanity but the social sub-system of economics, and link it to ecology. The sum of ecological economics is to align economic system structure and function to the structure and function of ecological systems, the focus is thus on the carrying capacity aspect of the environment. Works of Odum (1989) and Vitousek et al (1997) constitute the subline of inquiry on human well-being. In Odum, well-being relates to the Earth as a life support system: producing food, recycling water, assimilating waste and purification of air. Vitousek does not mention well-being, but the Earth model used places human activities at the top and forefront, and elements described are those that are vital (carbon, nitrogen) or have become harmful to life (harmful algal blooms). R^* is only vaguely addressed in this branch of inquiry and is common to the whole of humanity, it does not address issues of distribution and equality that are key to consumer-resource models (Box 2.1). The works of Odum (1989) and Costanza (1991) lead to concepts of Ecosystem Services (Daily, 1997), Natural Capital (Jansson et al., 1994), and Ecological Footprints (Wackernagel, 1998). Although these concepts are products of a similar body of research, the PBc distances itself from their approaches by removing the notion of values (ecosystem services and natural capital), and independent individual limits (footprints).

Resilience thinking in this genealogy has its origins in environmental sciences, but aims to integrate social and ecological processes and understands thresholds in both human and environmental systems. Thresholds in the social system encompass more than basic physiological needs, they can be thresholds in economic or political processes. In such integrated systems, where resilience is specified as 'resilience *of what, to what*?' (Carpenter et al., 2001b), carrying capacities (K) and minimum resource requirements (R^*) are highly contextual but are framed as more systemic limits to '*basins of attraction*' (Gunderson et al., 2002), found where resilience reaches zero. The PBc builds heavily on this body of research: the Safe Operating Space of Holocene-like Earth system dynamics represents a social-ecological basin of attraction. The resilience of this Safe Operating Space is being eroded along multiple axes of environmental degradation - the PBc's eleven Earth system processes, most of which are 'slow variables' – that act to change the overall size/resilience of the basin of attraction. The selection of these processes comes from Earth system sciences and represent (human impacted) Earth system processes. Social system processes are not included in those that might erode the resilience of the Safe Operating Space.

2.3.5 Interpreting the PBc in terms of resource scarcity versus waste accumulation

Four of the PBc's Earth system processes are resource depletion problems, and the remaining seven are waste accumulation problems (see Table 2.1). For instance, the planetary rate of anthropogenic carbon dioxide emissions exceeds the biosphere's ability to sequestrate it (Hansen, 2008; Anderies et al., 2013) while aquatic ecosystems are receiving higher loads of nitrogen and phosphorus than they can absorb (Chang et al., 2019b).

In the genealogy outlined here, waste accumulation is first described as a geological process (Marsh, 1874; Vernadsky, 1986), not as a human impact on the Earth system threatening humanity's own existence. However, Carson's 'Silent spring' (Carson, 1962) brings attention and interest in the problem of chemical pollution – her work is cited 13 times in this genealogy alone (see Table A2.2) is understood as a critical issue for the environment and people (Unesco 1968) and is seen as a turning point in the sustainable development policy world (Creech, 2012). Waste accumulation – or pollution – as a systemic and global problem appears in Boulding (1966): "*Oddly enough, it seems to be in pollution rather than in exhaustion that the problem is first becoming salient. Los Angeles has run out of air, Lake Erie has become a cesspool, the oceans are getting full of lead and DDT, and the atmosphere may become man's major problem in another generation, at the rate at which we are filling it up with gunk. It is, of course, true that at least on a microscale, things have been worse at times in the past. The cities of today, with all their foul air and polluted waterways, are probably not as bad as the filthy cities of the pretechnical age. Nevertheless, that fouling of the nest which has been typical of man's activity in the past on a local scale now seems to be extending to the whole world society; and one certainly cannot view with equanimity the present rate of pollution of any of the natural reservoirs, whether the atmosphere, the lakes, or even the oceans*". Boulding blames pollution on a flaw in the economic system that could be regulated through taxes.

What characterises pollution or waste is not the same across references however. Lovelock, 1979 frames waste as a necessary system dynamic throughput. A ban or tax on pollution would therefore be against natural order, but Lovelock blames a lack of sensibility for not ‘*putting industrial waste to good use*’. In Hardin (1963)’s understanding of cybernetic feedbacks, he addresses only natural waste, and calls for both its qualification and quantification. Limits to growth (Meadows et al., 1972; Meadows, 2004) call to not produce those substances that cannot be processed by the biosphere, reducing emissions rates of other substances, and re-using materials. The PBc thus builds on the science underlying systemic impacts of waste accumulation, and selects the chemical pollution as boundary category (Rockström et al., 2009b , – now labelled 'Novel entities' in Steffen et al., 2015), representing both natural and synthetic matters . However, the PBc does not build on Boulding (1966) or Lovelock's (1979) perspectives to understand the social *processes* (e.g. taxation/economic system, incentives, ‘sensibilities’) that underlie excess, synthetic and/or toxic wastes, perhaps explaining why the ‘chemical pollution/novel entities’ category remains different to other PBc waste accumulation processes.

2.4 Discussion

2.4.1 The inquiries

Holling sowed the seed of the Planetary Boundaries concept in 1973, as his work influences all the branches of inquiry. The Earth systems understanding behind the Planetary Boundaries was in place already in 1986: The Bretherton diagram (NASA Advisory Council 1986, National Research Council 1988) brought together all Earth system processes, Clark *et al* (1986) compiled essential impacts of humanity and questions relating to the needs for humanity. This work built on Spaceship Earth (Boulding 1966), that framed the ultimate global limit of the single Earth system and repercussions for economic systems. Burton and Kates' (1986) work ‘The Great Climacteric, 1798-2048: the Transition to a Just and Sustainable Human Environment’ also provided inspiration to the titles of modern day sustainability concepts (Rockström et al., 2009b; Vince, 2012; Raworth, 2017). The 1968 Biosphere conference already brought to light the risk of irreversible changes that would threaten the welfare of present and future generations (Unesco 1968). Since 1986, the cited science has provided consolidation and framing. Crutzen (2002) for instance put the Earth system science and social impacts work together in his framing of the Anthropocene, which in turn justifies the safe space of the concept as the Holocene. The resilience work, from Scheffer *et al* (2001) to Biggs *et al* (2009) outlines the possible scenarios of overshooting boundaries, and the efforts necessary to stay within them. Much of the knowledge behind this work was already explicit in Sustainable development of the Biosphere (Clark *et al* 1986), where Holling first presented the adaptive cycle delineating the system dynamic phases of collapse and reorganisation (Holling, 1986).

2.4.2 Relative or absolute limits?

We have described more than two centuries’ worth of research aiming to constrain human activities within environmental limits, culminating in the PBc. Science has made great progress in understanding the scale, extent and consequences of unsustainable development. Nonetheless, continued increases in humanity's negative impacts on nature – its life support system – justifies repeating and expanding the science. We now discuss some of the ways in which the different environmental limits have been relativized in practice, in a way which perhaps undermines the warnings that emerge from scientific research, and justifies ever more research to demonstrate that human impacts on the natural environment are deleterious to human well-being.

In ecological economics, the environment is often framed as natural capital. Under this framing, the extraction limit of non-renewable resources is set as the rate at which renewable substitutes are being created (Jansson et al., 1994). This implies that the real limit is not the non-renewable stock, but the creation of renewable substitutes, which is a technological issue. According to Moore's law, the observation that computers double in power every two years, technological advances know no limits (Moore, 2006).

Limits to the extraction of renewable resources are often quoted as set by the regeneration rate of resources and assimilation rate of waste (Jansson et al., 1994). However, such 'maximum sustainable' rates are not a constant, but a dynamic, system property (Odum 1989, Arrow *et al* 1995, May 1971). Also, there is a tendency to overshoot such limits (Odum 1989), which in itself has consequences on the future dynamics of the resource in question and its broader system (Carpenter et al., 2001a; Carpenter et al., 2008), and thus its maximum sustainable limit of (Holling, 1973; Clark et al., 1986).

Furthermore, when systems reorganise and restructure in response to resource stock collapses, baselines against which we measure the desired ecosystem dynamics or novel ecosystem services used also shift. For example, leading to the mid 1980s, Lake Victoria saw the rapid extinction of hundreds of native fish species and the upsurge of introduced Nile perch. The food web of Lake Victoria's ecosystem has adapted to the absences and presences of species, and lakeshore societies have transformed to social-economic systems that depend largely on Nile perch and the new food web. Management is now designed to manage fishing to the sustainable limits of the introduced species, not to recover previous species (Downing et al., 2014). This example illustrates that the parallel R*, the needs of the population – or the ecosystem and resources we aim to maintain – can also shift (Mooij et al., 2019).

The relativizations described above have perhaps in part shaped the scientific enquiry in a 'Red Queen's Race', where for each limit overshot, shifted or relativized, a new context for which to make the limit absolute has been sought. Perhaps in part also, the scientific method has shaped this line of inquiry by rejecting the null-hypothesis: first seeking the contexts in which a certain limit does not apply, then seeking the limits to new and yet unbound contexts.

The apparent contradiction between relative – and therefore potentially extendable – limits at sub-global levels and the absolute limit of the single planet is partly resolved in the literature that the PBc builds on: limits to sustainability are not carrying capacities to individual resources, or ecosystems but thresholds to system *dynamics*. Sustainable development seeks to produce those system dynamics in which societies can fulfil their needs and reap necessary resources in a way that supports the environment's ability to provide to these needs over time (Bretherton commission 1987). There is only one Earth for humanity (Boulding, 1966; Ward, 1972), and the Earth system is not self-regulating for human well-being (c.f. Lovelock 1979, Costanza 1991), especially not when human impacts affect precisely those processes that enabled human life to develop in the first place. Therefore, sustainable development is not – and most certainly not only - about limits, it is about the processes and interactions that shape long term human survival and well-being. Sustainable development isn't the answer to the question '*How much?*' but to the question *'How?'*. This is briefly explored in Odum (1989), who calls for an 'about-face' to focus on managing to improve system inputs rather than maximising system outputs. Bretherton, Rockström et al and Steffen et al. argue that determining how or what societies should do is beyond the remit of their disciplines (but see Rockström et al., 2017, Steffen et al., 2018). Yet, establishing what not to do has insufficient impact.

2.4.3 What is sustainable and what kind of sustainability do we want?

The system identified as sustainable in the PBc is one where Holocene-like Earth system dynamics prevail. The assumption that Holocene-like dynamics are safe is based on a) the relative stability of the Holocene, b) the knowledge that societies did develop and thrive during this epoch and c) research pointing to the Earth system dynamics produced by current trends as being inhospitable for humanity (Richardson et al., 2011; Steffen et al., 2015; IPCC, 2018). However, the PBc only assumes that Holocene-like Earth system dynamics are safe for all of humanity: *how* 8 billion people and counting can all be safe in Holocene-like dynamics, and maintaining those dynamics in the long run remains to be analysed. In short, Holocene-like Earth system dynamics is Rockström et al's (2009a) answer to the question '*what is sustainable?'.*

What constitutes sustainability - or the contexts or system dynamics that one wishes to maintain – is a normative choice. As stated in Clark *et al* (1986): *'If we accept the garden image as a useful one, two questions arise: What kind of garden do we want? What kind of garden can we get? The first of the questions - "What kind of garden do we want?" - ultimately calls for an expression of values. The values on which we have based this study - the kinds of garden we want - are suggested in our choice of title:* The Sustainable Development of the Biosphere*. The common sense meaning of "sustainable" is a good first approximation of our intended meaning. We seek to distinguish gardening strategies that can be sustained into the indefinite future from those that, however successful in the short run, are likely to leave our children bereft of nature's support.'*

The main message of the PBc is that current unsustainable trends in the Earth's social-ecological system increase the risks of passing thresholds beyond which these systems dramatically change structure and function. These new structures and functions may not be suitable for human life. More importantly: they may not be suitable to providing equal and sufficient quality of life to all. With this point, we touch on the PBc's Achilles' tendon: The Safe Operating Space does not effectively address R^* - i.e. the issue of resource distribution for all of humanity.

R^* is better represented in the social foundations of Doughnut economics (Raworth, 2017), where equity, equality, justice and the distribution of resources to all feature as necessary complements to environmental limits. These social foundations however remain void of context, expressed at a global level, and are thus difficult to implement.

An issue that remains to be resolved is thus in first focusing on the 'we' at sub-global levels, rephrasing Clark *et al* (1986)'s question to: *what gardens does who want*? To subsequently address the question of global sustainable development: *how* can the diverse and evolving understandings of sustainability be combined to achieve sustainable development for all? The combinations and compatibility of diverse and different perspectives of sustainability face many political and ethical challenges, and these are fields of research and knowledge that are absent from the PBc's genealogy. Indeed, even topics of equality and equity are hardly addressed in the genealogy (but see Majone, 1986) and not in the PBc (Steffen et al., 2015). It is important to recognise that the scientific genealogy that the PBc rests upon is deeply intertwined at its deepest roots: the authors of the work in the genealogy are part of a same school of thought, co-authors in each other's articles and books. A majority of the authors in this genealogy are male, from Europe and North America. This review – highlighting a stagnation in innovation since the 1980s – illustrates that little more progress can be made in understanding or guiding sustainable development without properly integrating the normative questions of resource and opportunity distribution. Addressing these questions appropriately must be done from a larger variety and diversity of perspectives than has shaped the PBc's genealogy.

2.4.4 The stories

Much of the literature presented here has been part of and influenced high level political fora, yet despite such high visibility the message has failed to yield sufficient response, much like Cassandra's dilemma.

One possible reason why scientific forecasts are seemingly ignored, could be - as outlined above - that they are not tackling the questions that can be acted upon:

understanding *what* is sustainable (rather than what isn't) for a diversity of people, not just humanity, and *how* sustainability can be achieved.

A related issue lies in identifying human needs. Earth system sciences focus on needs for food, water and (clean) air. Multiple Earth system processes contribute to providing these resources, and human development ought not to compromise those supporting services. However, the direct quest to meet these needs is not the only nor the root cause of environmental degradation, but rather the social systems that have been designed around the provision of these environmental services: economic systems' unbounded growth, farming systems' pesticides, technological systems' waste for example. It is in the first place *how* basic needs are met that is unsustainable. Humanity's development comes with many complex and evolving needs. These needs are context specific, where contexts include past dynamics (e.g. the need for justice), local conditions, and external drivers (e.g. market prices for resources).

In addition, all needs have never been met by everyone: famine and the effects of drought have existed throughout the Holocene, as have poverty and conflict. Development during the Holocene was not sustainable, hence reaching a Safe Operating Space is not simply returning to Holocene-like dynamics, rather it is (re-)creating Holocene-like dynamics with transformed social-ecological system interactions and processes.

Finally, unsustainability is often framed as a problem of the future, that might be solved by technologies and knowledge of the future. Nonetheless, the processes that need to be transformed - of unsustainable extraction, waste production and of inequitable distribution of resources, power and opportunities - are problems of today. Silent spring (Carson, 1962) and the hole in the ozone layer led to concrete actions (Creech, 2012). Both of these described immediate existing problems. The risks and consequences of overshooting planetary boundaries are serious and would likely lead to a no-return: to engage change for sustainable development, we need to focus on why unsustainable development is a serious issue today.

We highlight above that part of the problem in effectively conveying the message of limits to sustainability, is that these limits are easily relativized and stripped of their contexts, and that baselines for what needs to be sustained also shift. Furthermore, the global perspective, in which all of humanity would theoretically be safe under Holocene-like dynamics, possibly only reflects a form of retrogressive development, in which few people see an improvement to their well-being and livelihoods. Issues of equality and fairness that are fundamental to sustainable development are absent in a single, global humanity: scaling and determining operating spaces that are safe and just to appropriate contexts is essential.

Sustainability is not about warning of what not to do, rather it lies in determining what to do, and sustainable development addresses *how* to do it: understanding the dynamics of systems and flows. Extractive, consumptive and production systems ought to be designed to support an economy based on re-generation, not (quantitative) growth (Raworth 2017). Technology ought to be designed to support and maintain flows of matter, for instance by minimising, re-using, or properly treating waste and thus slowing waste accumulation, not maximise extraction. Circular economic models that redesign today's dominant linear growth economic models have evolved in parallel to the development of the science behind PBc, and they are also largely inspired by Boulding's Spaceship Earth (Maître-Ekern 2018). Such models, based on reducing raw material inputs and waste and pollution, are essentially supportive of an economy that reduces society's pressure on planetary boundaries. Yet circular economic models do not explicitly address sustainable levels of impacts. Importantly, implementing these transformations in the design of sustainable social-economico-technical systems needs to account for social justice, distribution and inequalities (Odum, 1989; Leach et al., 2010; Raworth, 2017).

2.5 Conclusions

As early as the 1960s (Carson, 1962; Unesco, 1968), and as late as the 1980s (United Nations 1987, Clark *et al* 1986, NASA Advisory Council 1986), all the messages of: a) irreversible damage of humanity's life support systems (at all scales) caused by human activities, b) the need for integrated interdisciplinary research to understand and achieve sustainable development and c) the crucial issues of equality and distribution for sustainability were well established in policy and scientific arenas. In this sense, the PBc rests on solid foundations. However, in this same sense, PBc does not appear to bring novel perspectives and solutions to the table. Scientific advances have allowed to decrease granularity and add some degrees of precision as to how unsustainable environmental degradation is and the risks posed by this degradation. However, by still not addressing the diverse and dynamic sources of social drivers and impacts on sustainability, PBc risks facing Cassandra's dilemma.

Defining and securing sustainable futures for all, across scales and reframing the narrative of sustainable development away from Cassandra's dilemma will require not only solid scientific foundations. It will also require broad foundations that are representative of the diversity of perspectives that shape and are shaped by (sustainable) development. It will require diverse and innovative perspectives, and one might argue that the first step in innovation is a step beyond the narrow box of perspectives so far included. Fields of ethics and humanities are mostly absent in the PBc, but are essential to tackling the challenges of determining sustainability across scales of space and time.

Understanding how social-ecological initiatives and processes combine and co-evolve to influence sustainable development ought to be within the mandate of scientific research: there is no evidence to suggest that scientists have been cursed in the same way as Cassandra, knowledge acquired through scientific research can and ought to be made useful to and usable by societies by both scientists and policymakers.

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Chapter 3

A Generically Parameterized model of Lake eutrophication (GPLake) that links field-, lab- and model-based knowledge

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Abstract

Worldwide, eutrophication is threatening lake ecosystems. To support lake management numerous eutrophication models have been developed. Diverse research questions in a wide range of lake ecosystems are addressed by these models. The established models are based on three key approaches: the empirical approach that employs field surveys, the theoretical approach in which models based on first principles are tested against lab experiments, and the process-based approach that uses parameters and functions representing detailed biogeochemical processes. These approaches have led to an accumulation of field-, lab- and model-based knowledge, respectively. Linking these sources of knowledge would benefit lake management by exploiting complementary information; however, the development of a simple tool that links these approaches was hampered by their large differences in scale and complexity. Here we propose a Generically Parameterized Lake eutrophication model (GPLake) that links field-, lab- and model-based knowledge and can be used to make a first diagnosis of lake water quality. We derived GPLake from consumer-resource theory by the principle that lacustrine phytoplankton is typically limited by two resources: nutrients and light. These limitations are captured in two generic parameters that shape the nutrient to chlorophyll-a relations. Next, we parameterized GPLake, using knowledge from empirical, theoretical, and process-based approaches. GPLake generic parameters were found to scale in comparable manner across data sources. Finally, we show that GPLake can be applied as a simple tool that provides lake managers with a first diagnosis of the limiting factor and lake water quality, using only the parameters for lake depth, residence time and current nutrient loading. With this first-order assessment, lake managers can easily assess measures such as reducing nutrient load, decreasing residence time or changing depth before spending money on field-, lab- or model- experiments to support lake management.

3.1 Introduction

Severe eutrophication may lead to phytoplankton blooms that plague societies around the world (Hallegraeff, 1993; Heisler et al., 2008; Schindler, 2012). Action to reduce eutrophication is urgent because phytoplankton blooms pose risks to drinking water and lead to ecosystem degradation (Carpenter et al., 1998; Qin et al., 2010). Since managers spend much effort and money on measures to improve water quality (Thornton et al., 2013), they would benefit from a simple tool that quickly provides insight into phytoplankton concentrations under different nutrient loads for a wide range of lakes. This insight provides a way to assess the amount of effort needed in nutrient load reduction to meet water quality standards (Jeppesen et al., 2007c; Janssen et al., 2017). Many researchers have tried to develop such tools, each using different types of knowledge with their respective data sources, methods and approaches (Huisman et al., 2002; Schindler, 2006; Cuddington et al., 2013; Janssen et al., 2015).

Half a century ago, when the first signs of 'cultural eutrophication' became increasingly evident, scientists started developing models to support lake management (Vollenweider, 1968; Jones et al., 1986; Schindler, 2006; Thornton et al., 2013). Due to limited computing power and understanding of mechanisms at that time, the study of lake eutrophication was limited to the approach of simple regression analysis based on data from field measurements and lake characteristics. For example, empirical models such as Vollenweider's model (Vollenweider, 1975) estimate the trophic state of lakes and give general recommendations for the extent to which nutrient loading should be limited to maintain a healthy state (Ogawa, 1977; Vollenweider, 1982; Costanza et al., 1983; Brett et al., 2008). Although these empirical models are transparent in their calculations, their reliability can be lost when applied beyond their calibration domain (Cuddington et al., 2013; Janssen et al., 2019a). As a result, many versions of Vollenweider's model have been proposed in different contexts; however, each is limited to its own calibration domain (Reckhow et al., 1983; Kimmel et al., 1984; Nürnberg, 1984; Lijklema et al., 1989; Carpenter et al., 1995).

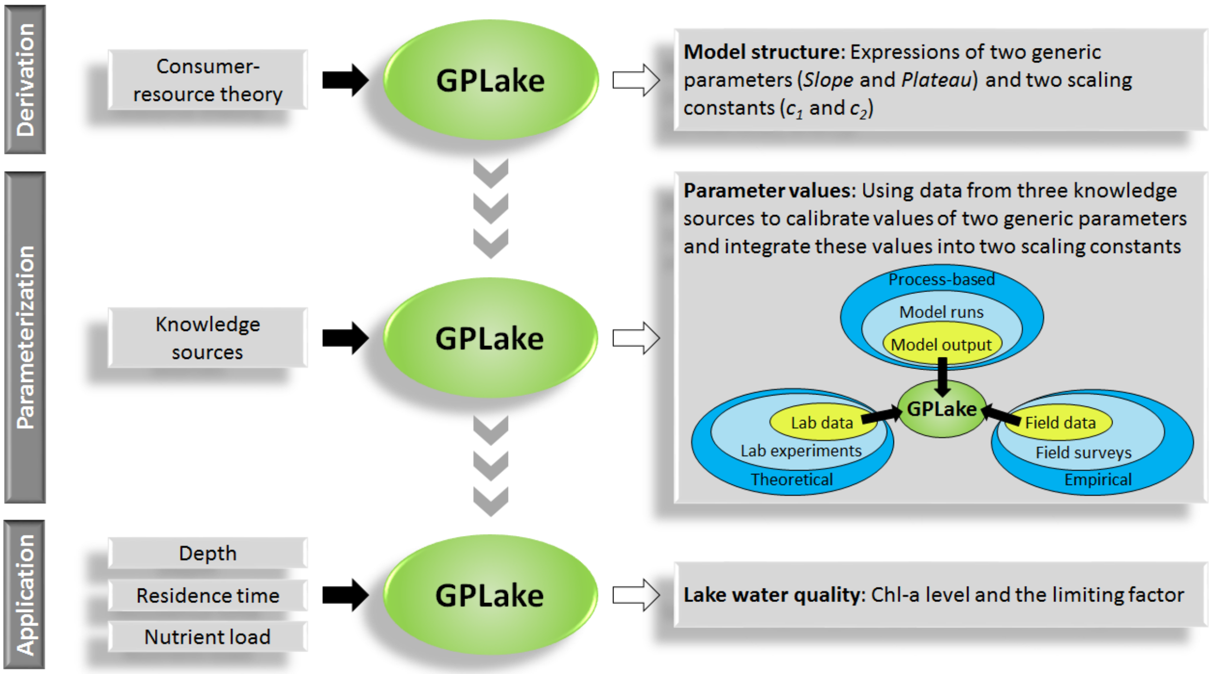
A second approach, that of theoretical models, was developed based on first principles. These first principles are, for example, based on mass or energy flows, thereby describing consumer-resource interactions using clear mathematical equations (Tilman, 1982; Huisman et al., 1999). These models are tested against and supported by data from comprehensive laboratory experiments and describe the relationship between nutrient and phytoplankton concentration by fundamental mechanisms (Tilman, 1977; Sommer, 1989; Evers, 1991; Huisman et al., 1994; Huisman et al., 2002). However, it is hard to apply theoretical models to predict the impacts of eutrophication for real cases due to the models' abstractness.

Last but not least, a third approach emerged, that of process-based models. Process-based models are valuable, as they are based on a mechanistic understanding of ecosystems, which results in high flexibility when applied to lake management questions (DeAngelis et al., 2003; Robson et al., 2008; Cuddington et al., 2013). Process-based models are well suited for scenario analyses for management strategies, as has been shown by various applications with PCLake (Mooij et al., 2007; Janse et al., 2010; Janssen et al., 2017) and many other models (Cuddington et al., 2013). Nevertheless, understanding the model and measuring its parameters is complex and demanding.

Linking knowledge obtained from empirical, theoretical and process-based approaches in one generic model can be beneficial to lake managers for three reasons. First, such a model will rely on an empirical approach, collecting data through field surveys and make predictions based on correlations. The empirical approach, by its nature of deriving predictions from field data, is inherently realistic without further effort. Second, a generic model will encompass the knowledge from a theoretical approach that uses first principles and laboratory experiments. Incorporation of this knowledge increases the transparency of underlying mechanisms that lead to trophic states in lakes. Third, the generic model will incorporate mechanistic knowledge from a process-based approach. This increases the flexibility of its application since it is not limited to a calibration domain. Managers will thus benefit from the realism, transparency and flexibility when knowledge obtained with these three approaches is linked. Such a model will be widely applicable to lakes, including those lakes that have not been subjected to rigorous empirical study due to their geographic location or monetary constraints.

In this paper, we propose a Generically Parameterized model of Lake eutrophication (GPLake) that links field-, lab- and model-based knowledge. Field-based knowledge arises from an empirical approach in which field data are collected during field surveys. Lab-based knowledge is obtained when theoretical first principles are tested using data gathered in lab-experiments. Model-based knowledge is captured in the structure, parameters and functions of process-based models that produce model output and consequently provide ecological insight through model runs.

The basis of this GPLake model is derived from Tilman's resource competition model, which explains species nutrient limitation by applying the R^* theory (Tilman, 1982), and the Huisman et al. light competition model (Huisman et al., 1994; 1995; Huisman et al., 2002), which accounts for the effects of light limitation on phytoplankton species using the so-called I_{out}^* theory (Figure 3.1, GPLake derivation). The resulting expressions for GPLake are parameterized by capturing the essential information of field-, lab- and model-based knowledge (Figure 3.1, GPLake parameterization). Finally we showcase with a hypothetical lake that GPLake can be applied as a simple tool to provide lake managers with a first diagnosis of limiting factors and lake water quality, using only the parameters lake depth, residence time and nutrient load (Figure 3.1, GPLake application).



Model structure: Expressions of two generic parameters (*Slope* and *Plateau*) and two scaling constants (c_1 and c_2)

Parameter values: Using data from three knowledge sources to calibrate values of two generic parameters and integrate these values into two scaling constants

Lake water quality: Chl-a level and the limiting factor

Figure 3.1 Schematic structure of the derivation, parameterization and application of GPLake (green oval). In the derivation step, consumer-resource theory is used to derive the expressions of GPLake that consist of two generic parameters. In the parameterization step, the GPLake model links field-, lab- and model-based knowledge that emerges from three levels: the conceptual approach level (dark blue oval), technical method level (light blue oval) and observational data level (yellow oval). In the application step, GPLake is applied using only the lake characteristics depth, residence time and nutrient load.

3.2 Methods

3.2.1 Theoretical background for GPLake

In the 1980s, Tilman (1982) developed his seminal resource competition theory. This theory was extended by Huisman and Weissing (1994; 1995) in the 1990s by adding light as a heterogeneous resource in the water column. According to Huisman's theory the ecosystem will go through three phases while nutrient loading is increasing: the *Zero-growth-phase*, the *Nutrient limitation phase* and the *Light limitation phase*. The phytoplankton concentration at equilibrium W^* and the nutrient concentration at equilibrium R^* for each of the phases are as follows (for the model symbols and descriptions for communities of phytoplankton see Table 3.1):

Zero-growth phase: In this phase nutrient loading is too low to support species growth and all the inflowing nutrients will remain in their inorganic form. Hence the phytoplankton concentration at equilibrium W_0^* is zero, and the nutrient concentration at equilibrium R_0^* equals the inflowing resource concentration R_{in}.

$$W_0^* = 0, \tag{3.1a}$$

$$R_0^* = R_{in}. \tag{3.1b}$$

Nutrient limitation phase: In this phase the phytoplankton is able to deplete the inflowing resource concentration R_{in} and becomes nutrient limited. As a result, the equilibrium phytoplankton concentration W_1^* has a linear relationship with nutrient loading minus remaining resource concentration R_1^* and dilution rate D (reciprocal of the residence time), and an inverse linear relationship with phytoplankton community loss rate l and phytoplankton community stoichiometry c. The remaining resource concentration at equilibrium R_1^* depends on the phytoplankton community growth rate p_{max}, the phytoplankton community loss rate l and the phytoplankton community half-saturation constant for nutrient uptake H_R.

$$W_1^* = \frac{D\ (R_{in} - R_1^*)}{lc}, \tag{3.2a}$$

$$R_1^* = \frac{l\ H_R}{p_{max} - l}. \tag{3.2b}$$

Light limitation phase: In this phase the phytoplankton is light limited due to the excessive phytoplankton concentration enabled by high nutrient loading. The equilibrium phytoplankton concentration W_2^* becomes a constant number even at increasing nutrient loading because the excessive phytoplankton concentration leads to self-shading that prevents further phytoplankton growth. Here, W_2^* is dependent on the depth z, the incident irradiance I_{in}, the light intensity at bottom of water column at equilibrium I_{out}^*, the phytoplankton community half-saturation constant for light uptake H_L, the phytoplankton community extinction coefficient k, the phytoplankton community loss rate l and the phytoplankton community maximum growth rate p_{max}. Here, I_{out}^* obeys Lambert-Beer's law stating that absorbance is directly proportional to the thickness of the water layer: $I_{out}^{*} = I_{in}\, e^{-kW_2^{*}z}$. In this phase the equilibrium resource concentration R_2^{*} is proportional to inflowing resource concentration *R_{in}*, since the excessive nutrients can no longer be taken up for phytoplankton growth.

$$W_2^{*} = \frac{p_{max}}{zkl} ln \frac{H_L + I_{in}}{H_L + I_{out}^{*}}, \tag{3.3a}$$

$$R_2^{*} = R_{in} - W_2^{*} \frac{lc}{D}. \tag{3.3b}$$

Table 3.1 Model symbols and descriptions used in this study

Symbol	Unit	Description	Category
$Slope$	mg mg^{-1}	Phytoplankton concentration over inflowing resource concentration at equilibrium in the nutrient limitation phase	Generic parameter
$Plateau$	mg m^{-3}	Phytoplankton concentration at equilibrium in the light limitation phase	Generic parameter
$R_{in,switch}$	mg m^{-3}	Inflowing resource concentration at which nutrient limitation will switch to light limitation	Auxiliary parameter
R_{in}	mg m^{-3}	Inflowing resource concentration	Input variable
D	day^{-1}	Dilution rate (reciprocal of residence time)	Physical parameter
z	m	Depth	Physical parameter
I_{in}	W m^{-2}	Light supply intensity	Physical parameter
p_{max}	day^{-1}	Phytoplankton community maximum growth rate	Biological parameter
l	day^{-1}	Phytoplankton community loss rate	Biological parameter
c	g g^{-1}	Phytoplankton community stoichiometry	Biological parameter
k	m^{2} g^{-1}	Phytoplankton community extinction coefficient	Biological parameter
H_L	W m^{-2}	Phytoplankton community half saturation constant of light	Biological parameter
H_R	g m^{-3}	Phytoplankton community half saturation constant of resource	Biological parameter
W_0^*	mg m^{-3}	Phytoplankton concentration at equilibrium in the zero-growth phase	Output variable
W_1^*	mg m^{-3}	Phytoplankton concentration at equilibrium in the nutrient limitation phase	Output variable
W_2^*	mg m^{-3}	Phytoplankton concentration at equilibrium in the light limitation phase	Output variable
R_0^*	mg m^{-3}	Resource concentration at equilibrium in the zero-growth phase	Output variable
R_1^*	mg m^{-3}	Resource concentration at equilibrium in the nutrient limitation phase	Output variable
R_2^*	mg m^{-3}	Resource concentration at equilibrium in the light limitation phase	Output variable
I_{out}^*	W m^{-2}	Light intensity at the bottom of the water column at equilibrium	Output variable
c_1	day mg mg^{-1}	Phytoplankton concentration over inflowing resource concentration over dilution rate in the nutrient limitation phase	Scaling constant
c_2	mg m^{-2}	Phytoplankton abundance per unit of surface area in the light limitation phase	Scaling constant

3.2.2 Derivation of GPLake

The GPLake model is derived by first building the model structure and then deriving the expressions of the scaling constants. These scaling constants will be used to link data from the three knowledge sources. Below more details are given for each of the derivation steps.

3.2.2.1 GPLake model structure

To derive the model structure, we assume that nutrient limitation and light limitation are the two most important mechanisms that define the relationship between phytoplankton and nutrient loading (Figure 3.1, GPLake derivation). Therefore, we combine the aforementioned resource and light competition models to derive GPLake. We use the resulting GPLake equations (Equation (3.4-7)) to calculate phytoplankton and nutrient concentration at equilibrium; i.e., where phytoplankton and nutrient concentrations do not change over time because their derivatives equal zero. For details on the derivation of these equations please see Appendix 3.1. In our model we make the following assumptions to simplify our approach: 1) Because the minimal resource requirement to support the start of phytoplankton growth is tiny, we assume that the first phase of zero growth can be neglected (Rigler, 1956); 2) similarly, at the nutrient limitation phase, the minimum nutrient concentration required for phytoplankton growth R_1^* is assumed to be close enough to zero that the difference can be ignored here for practical purposes; 3) in the light limitation phase, where phytoplankton is limited by self-shading, we assume that light extinction caused by phytoplankton can make the I_{out}^* approximately zero. GPLake can thus be defined as a two phase model that describes the relationship between phytoplankton concentration and nutrient loading in two phases that are characterized by the limitation by one of two main resources, either nutrient or light (Cloern, 1999); i.e., GPLake obeys Liebig's law of the minimum. To derive the model, we need to know the relation between phytoplankton concentration and inflowing resource concentration under nutrient limiting conditions to set the *Slope* parameter of GPLake, and the maximum phytoplankton concentration at light limitation to set the *Plateau* parameter of GPLake. A graphical representation of GPLake is given in Figure 3.2.

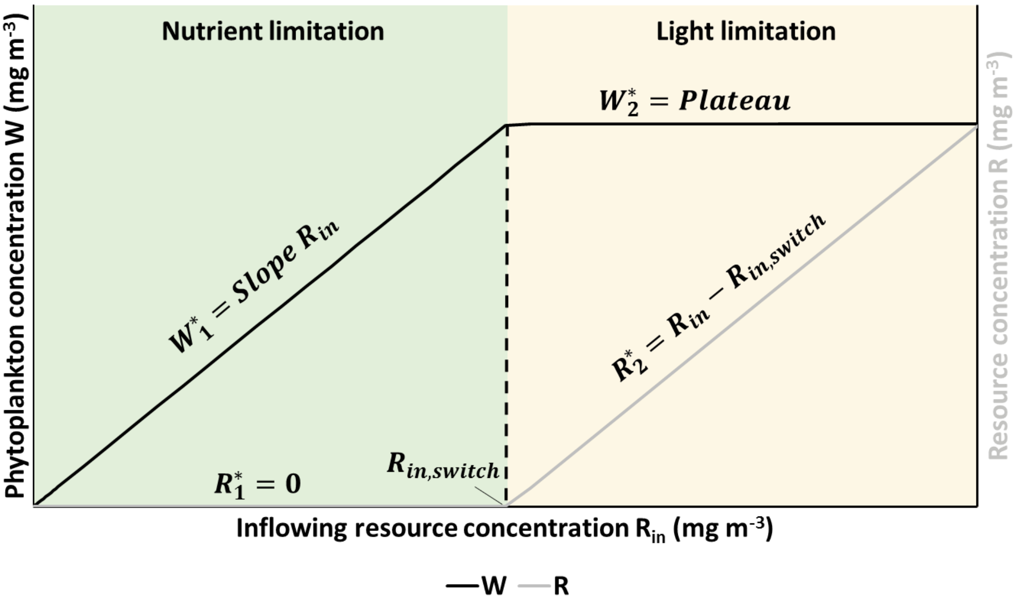


Figure 3.2 A graphical representation of GPLake. The response of both the equilibrium resource concentration (right Y-axis) and the equilibrium phytoplankton concentration (left Y-axis) on the inflowing resource concentration (X-axis). The figure shows the contrast between the nutrient limitation and the light limitation phase of the GPLake model. *$R_{in,switch}$* is an auxiliary parameter defined by *Slope* and *Plateau* and represents the inflowing resource concentration at which the model switches between these two phases. In the nutrient limitation phase, the phytoplankton concentration increases linearly with increasing nutrient loading. The *Slope* of the increasing phytoplankton concentration is determined by dilution rate, community loss rate and community stoichiometry. In the light limitation phase, the phytoplankton achieves a *Plateau* and excessive nutrients can no longer be taken up.

Based on Equation (3.2a) and Equation (3.3a), the *Slope* and *Plateau* of GPLake can be defined as:

$$Slope = \frac{D}{lc}, \tag{3.4a}$$

$$Plateau = \frac{p_{max}}{zkl} ln \frac{H_L + I_{in}}{H_L}, \tag{3.4b}$$

and the switch point of the inflowing resource concentration where the model changes from nutrient limitation to light limitation equals

$$R_{in,switch} = \frac{lc}{D} \frac{p_{max}}{zkl} ln \frac{H_L + I_{in}}{H_L} = \frac{Plateau}{Slope}. \tag{3.5}$$

Once the *Slope* and the *Plateau* are known, the phytoplankton and resource concentration at equilibrium under nutrient limitation ($R_{in} \leq R_{in,switch}$) can be calculated as:

$$W_1^* = Slope\ R_{in}, \tag{3.6a}$$

$$R_1^* = 0, \tag{3.6b}$$

and, in the case of light limitation ($R_{in} > R_{in,switch}$,) as:

$$W_2^* = Plateau, \tag{3.7a}$$

$$R_2^* = R_{in} - \frac{Plateau}{Slope} = R_{in} - R_{in,switch}. \tag{3.7b}$$

We need eight mechanistically interpretable parameters to determine the *Slope* and *Plateau* of GPLake (Table 3.1). Among them, the depth z, dilution rate D and light intensity I_{in} are physical parameters that depend on the lake characteristics, while the maximum growth rate p_{max}, loss rate l, extinction coefficient k, half saturation constant of light H_L and nutrient stoichiometry c are biological parameters that vary among phytoplankton species. Importantly, the biological parameters in the equations should be measured at the phytoplankton community level. To show the dependency of the output variables of GPLake on its parameters we performed a two-level analytical sensitivity analysis (see Appendix 3.2 for further details). The first level deals with the sensitivity of GPLake output variables, i.e. W_1^*, W_2^*, R_1^* and R_2^*, to the generic parameters *Slope, Plateau* and the auxiliary parameter $R_{in,switch}$ (Equation (3.6-7)). The second level deals with the sensitivity of the GPLake parameters: *Slope, Plateau* and $R_{in,switch}$ (Equation (3.4-5)), to the physical (D, z, I_{in}) and biological (p_{max}, l, k, H_L, c) parameters.

3.2.2.2 Linking knowledge from three sources

Within the derivation of GPLake we developed a method to link the knowledge from empirical, theoretical and process-based approaches. Next, the *Slopes* and *Plateaus* of GPLake were obtained from field data, lab data and from process-based model output to benefit from the complementary information they hold (Roebber et al., 2004; Tebaldi et al., 2007; Wang et al., 2011). To meet this challenge, we standardized the physical parameters that represent the characteristics of the systems for which we fitted GPLake. Assuming that incoming irradiance (I_{in}) is similar for each system, we defined two scaling constants c_1 and c_2 that depend only on the phytoplankton community composition. As such, an increase in dilution rate or depth should result, respectively, in an increase of the *Slope* or a decrease of the *Plateau*:

$$c_1 = \frac{1}{lc} = \frac{Slope}{D}, \tag{3.8a}$$

$$c_2 = \frac{P_{max}}{lk}\ ln\ \left(\frac{H_L + I_{in}}{H_L}\right) = z\ Plateau. \tag{3.8b}$$

Both constants can be calculated using the GPLake *Slope* and *Plateau* obtained by using data of each source of knowledge while using the depth and dilution rate of the same source of knowledge as scaling factors.

Table 3.2 Depth, residence time and dilution rate of the different data sources

Data type	Data source	Mixed water layer depth (m)	Residence time (d)	Dilution rate (d^{-1})
Field[a]	Vollenweider[b]	10.0	1460	6.85E-04
	Janse	2.02	171	5.85E-03
Lab	Marinho: LEA	0.05	8.33	0.12
	Marinho: MIRF	0.05	8.33	0.12
	Marinho: CP	0.05	8.33	0.12
	Marinho: CS	0.05	8.33	0.12
Model	Model runs[c]	2	100	0.01

[a] **The values for field data sets represent averaged values.**

[b] **Depth and dilution rate for the Vollenweider data set were estimated using expert judgement based on lake types included in the data set, as these variables are not specified.**

[c] **The model settings are described in Appendix 3.3.**

3.2.3 Parameterization of GPLake

To optimize its applicability to practical eutrophication problems, we parameterized GPLake with field data, lab data and model output that relate respectively to empirical, theoretical and process-based approaches (Figure 3.1, parameterization). We linked these three data sources for comparable ranges of nutrient loadings that are normalized by water depths and dilution rates using the Vollenweider method shown by Equation (3.9) (Table 3.2) (Vollenweider, 1975; Jones et al., 1988). Here P is the normalized P loading in mg P m^{-3}; $L(P)$ is the annual total phosphorus load per unit of surface area in mg P m^{-2} year^{-1}; q_s is the mean depth divided by the hydraulic residence time in m year^{-1}; and τ_w is the hydraulic residence time in years. Here the residence time can be calculated by dividing the total volume of water by the water flux into the lake.

$$P = \frac{L\,(P)}{q_s\left(1 + \sqrt{\tau_w}\right)} \tag{3.9}$$

3.2.3.1. Parameterization of GPLake with field data

To parameterize GPLake with field data we calibrated the two generic parameters of GPLake, the *Slope* and *Plateau*, using two field data sets. One field data set is the one compiled by Vollenweider, which includes numerous deep lakes that are situated around the globe (Rast et al., 1978; Jones et al., 1986). The second data set has been compiled by Janse for the calibration of PCLake, which includes 52 shallow lakes in Europe (Janse, 2005). Please note that the latter data set also includes some lakes with a high vegetation coverage, while the Vollenweider data set comprises only phytoplankton-dominated lakes. The nutrient loadings of both the Vollenweider data set and the Janse data set were normalized by lake depth and dilution rate according to the Vollenweider method (Equation (3.9)) (Vollenweider, 1975; Jones et al., 1988). The calibration was performed using the *Generalized Reduced Gradient Non-linear* method included in the solver analysis tool of MS Excel to find the values of *Slope* and *Plateau* that can maximize the coefficient of determination R^2 between the GPLake prediction and the field data (Winston, 2016). After calibrating GPLake, we compared various measures of goodness-of-fit (R^2, RMSE and Bias) of the GPLake model with the regression model applied by Vollenweider (1975). In addition, we performed an uncertainty analysis of the fit of both models to the Vollenweider and the Janse data sets using a randomization technique. For details of uncertainty analyses see Appendix 3.4.

3.2.3.2. Parameterization of GPLake with lab data

To parameterize GPLake with lab data, we used the published lab data for chl-a concentration in a chemostat experiment that ran under both phosphorus limitation and light limitation (Marinho et al., 2013). To link GPLake with lab data it is important that the total light (I_{in}) in the laboratory is comparable to field conditions. We used published data from lab experiments for four strains of two phytoplankton species (*Microcystis aeruginosa* and *Cylindrospermopsis raciborskii*) isolated from four Brazilian lakes (Marinho et al., 2013). Lab data from other phytoplankton species can be applied to determine GPLake generic parameters using the same approach as we describe here. We determined the *Slope* in the nutrient limitation phase based on two values: one defined by the origin and the seccond by the chl-a concentration under a phosphorus limited nutrient load. This calculation is based on the assumption that the minimal resource requirement to support phytoplankton growth is sufficiently close to zero (Figure 3.2). The chl-a concentration under light limited conditions determines the level of the *Plateau*. The values of the inflowing resource concentration at the switch point $R_{in,switch}$ are calculated by Equation (3.5).

3.2.3.3 Parameterization of GPLake with model output

To parameterize GPLake with process-based model output, we selected PCLake as a model example. PCLake is a well-established eutrophication model used to simulate biogeochemical processes, including phytoplankton and nutrient dynamics in homogeneous shallow lakes (Janse, 2005). The default PCLake version (the full model can be found at GitHub: https://github.com/pcmodel) includes phytoplankton, zooplankton, fish, aquatic vegetation, inorganic and organic nutrients in the lake water column and accounts for interaction between these components and the sediment. For details on the model settings and parameters see (Janse, 2005). In this study, we used the default version of PCLake except that we excluded aquatic vegetation because it is a primary producer that competes with phytoplankton for nutrients. Including aquatic vegetation would violate the assumptions in GPLake on the relationship between phytoplankton and nutrients.

To make the output of the PCLake simulations comparable with field data sets, we used the normalized nutrient loading (Equation (3.9)) in the range of 1-1000 mg P m^{-3}, as in the Vollenweider data set (Vollenweider, 1975; Jones et al., 1988). We ran PCLake for nutrient loads with ranges of 1-10 mg P m^{-3}, 10-100 mg P m^{-3} and 100-1000 mg P m^{-3}, each with 20 equidistant intervals. Consequently, we ran PCLake for 60 simulations. We used the Vollenweider method (Jones et al., 1988), as described in Appendix 3.3, to denormalize the nutrient loading from 1-1000 mg P m^{-3} to the nutrient loading in the unit of mg P m^{-2} day^{-1} prescribed by PCLake. The resulting annually averaged chl-a levels at equilibrium of each simulation were reported. These simulation outputs were used to fit the two generic parameters of GPLake in the same way as was done for the field data sets (section 2.3.1). In addition, we performed simulations with different lake characteristics in PCLake to see how the GPLake *Slope* and *Plateau* vary between lake types with different physical, chemical and biological characteristics (for details and results see Appendix 3.3).

3.2.4 Application of GPLake

For the application of GPLake, the parameterized scaling constants c_1 and c_2 from the three data sources are used. Through these scaling constants the *Slope* and *Plateau* can be obtained for any lake to which GPLake is applied by adopting the lake specific depth z and dilution rate D:

$$Slope(D) = c_1 D, \tag{3.10a}$$

$$Plateau(z) = \frac{c_2}{z}. \tag{3.10b}$$

Hence, the first diagnosis can be made by lake managers by building the relations between chl-a levels and inflowing nutrient concentration R_{in}:

$$\begin{aligned} \text{Chl-a} &= min\big(Slope(D)\ R_{in}, Plateau(z)\big) \\ &= min\left(c_1 D R_{in}, \tfrac{c_2}{z}\right). \end{aligned} \tag{3.11}$$

Besides, the comparison between R_{in} and $R_{in,switch}$ (Equation (3.5)) can be used to estimate the limiting factor of lakes, i.e. nutrient limited if $R_{in} \leq R_{in,switch}$ and light limited if $R_{in} > R_{in,switch}$.

For illustrative purposes, we showcase an application for a hypothetical lake of 2 m depth and a dilution rate of 0.006 day^{-1} (residence time of 167 days). By applying GPLake to this hypothetical lake, the lake specific *Slope* and *Plateau* are obtained. This *Slope* and *Plateau* form a graph that gives a first assessment of the response of this lake to nutrient loading. With knowledge of the current nutrient load, a lake manager can make a first diagnosis of the lake water quality, e.g. chl-a level and limiting factors. Also, the lake manager can calculate the required reduction in nutrient load. Finally, GPLake can be applied to estimate the effect of measures such as a changed residence time or lake water level.

3.3 Results

3.3.1 Parameterization of GPLake

For a full parameterization of GPLake we first used the three sources of data (from field, lab and model) to estimate the generic parameters and the scaling constants. Next all estimates for the scaling constants are averaged. For each step we give details below.

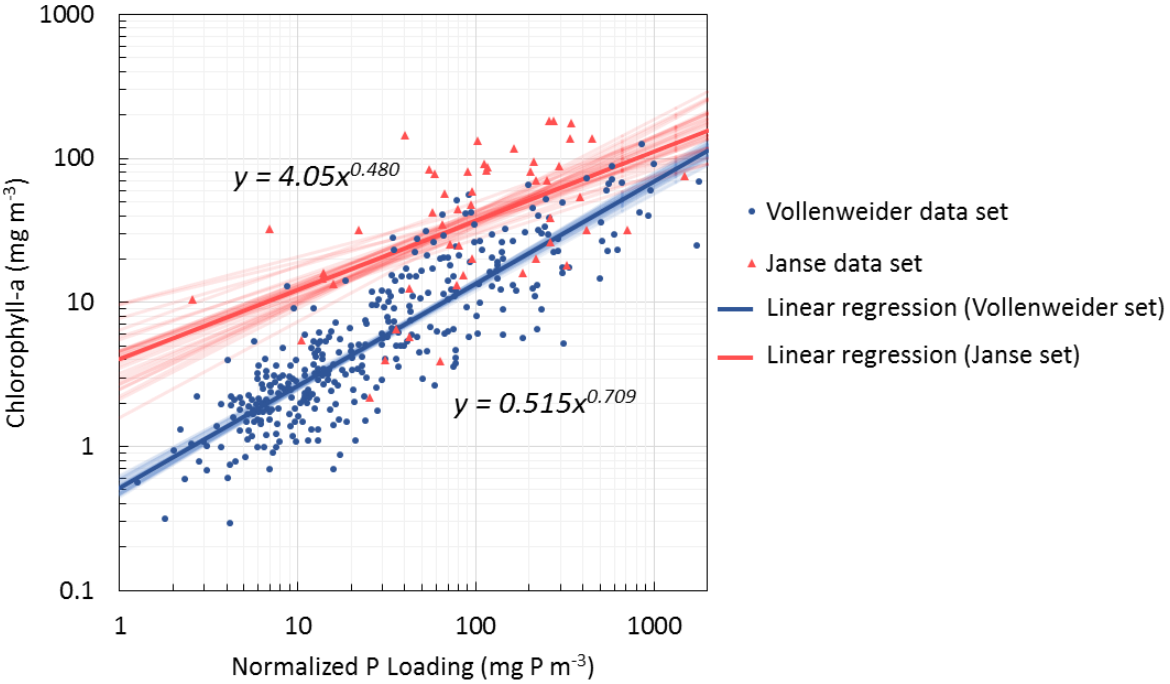


Figure 3.3 Linear regression models based on the log-log-transformed Vollenweider data set for > 300 water bodies (Jones et al., 1986) and the Janse data set for 52 shallow lakes in Europe, which data set was applied in the PCLake calibration (Janse, 2005). The Vollenweider data set and the Janse data set are shown by blue circles and red triangles, respectively, and the coloured lines show the regression model of the corresponding data set. The uncertainty of the models is illustrated by showing 30 model fits based on randomized data (transparent coloured lines). See Appendix 3.4 for details.

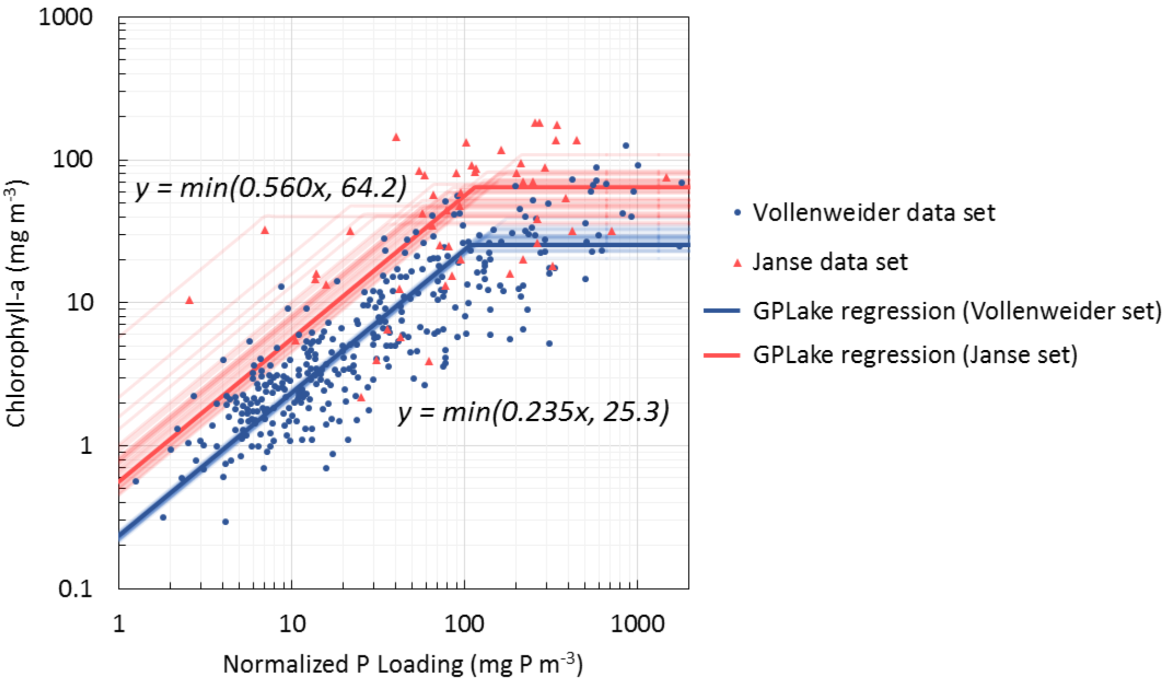


Figure 3.4 Results from GPLake regression based on the same data sets as in Figure 3.3. The two segmented lines show the GPLake calibration results for the Vollenweider data set for deep lakes and the Janse data set for shallow lakes. The result shows that the shallow lakes have a higher phytoplankton concentration at the point at which light becomes limiting. The uncertainty of the models is illustrated by showing 30 model fits based on randomized data (transparent coloured lines). See Appendix 3.4 for details.

3.3.1.1 Parameterization of GPLake with field data

First, we parameterized GPLake with field data to illustrate its link to a natural situation. Figure 3.3 shows the commonly applied method in empirical studies of linear regression in log-log space (i.e., estimating a power function in linear-linear space) to fit both the Vollenweider and Janse lake data sets (Vollenweider, 1975; Jones et al., 1986; Janse, 2005). Here, the Vollenweider data set refers mainly to deep lakes and the Janse data set refers to shallow lakes. Under the same normalized nutrient loading, the chl-a levels in shallow lakes (red triangles) are generally higher than in deep lakes (blue circles). This illustrates that depth inversely correlates with chl-a level. The maximum chl-a level (*Plateau*) also correlates inversely with depth, which suggests that our assumption that c_2 (Equation (3.8b)) is a constant is valid. When parameterizing GPLake, a larger *Slope* for the Janse data set was observed than for the Vollenweider data set, as shown in Figure 3.4. Consequently, phytoplankton concentrations in shallow lakes were more sensitive in its response to increasing inflowing nutrient concentration than in deep lakes. Shallow lakes often have lower residence time (i.e. higher dilution rates). This is consistent with our assumption about the scaling constant c_1 (Equation (3.8a)): an increase in dilution rate should be followed by an increase in *Slope* in order to keep c_1 constant. Table 3.3 shows that the linear regression model and GPLake are comparable in the goodness-of-fit.

Table 3.3 Comparison of the goodness-of-fit of the log-log linear regression model and GPLake to the Vollenweider and Janse data set

Data set	Model	R^2	RMSE	Bias
Vollenweider	Linear regression	0.75	0.26	-5.55E-07
	GPLake	0.72	0.28	2.27E-08
Janse	Linear regression	0.29	0.40	9.03E-07
	GPLake	0.23	0.42	-1.26E-04

3.3.1.2 Parameterization of GPLake with lab data

When GPLake was parameterized with lab data of Marinho et al., 2013, the GPLake generic parameters showed *Slopes* and *Plateaus* that were more similar within species than between species (Figure 3.5). The *Plateaus* reached by the *Microcystis* strains were lower than the *Plateaus* reached by the *Cylindrospermopsis* strains, indicating differences between these taxa in their physiology (e.g. different chl-a per cell volume in Marinho et al., 2013). Interspecific differences in *Slopes* may be expected among species, as species are known to be flexible and distinct in their stoichiometric composition (Droop, 1974; Sterner et al., 1992). Nutrient limitation is species-specific (Beardall et al., 2001), and for a correct estimation of the *Slope* it is imperative that phytoplankton indeed experiences nutrient limiting conditions in the chemostat (See Figure 3.5, CP as an example of non-limiting conditions). Intraspecific differences between *Slopes* and *Plateaus* of different strains are likely the result of a high variability among the strains' traits within the species, which is, for example, reflected by the variability in the growth of *Microcystis* strains (Marinho et al., 2013).

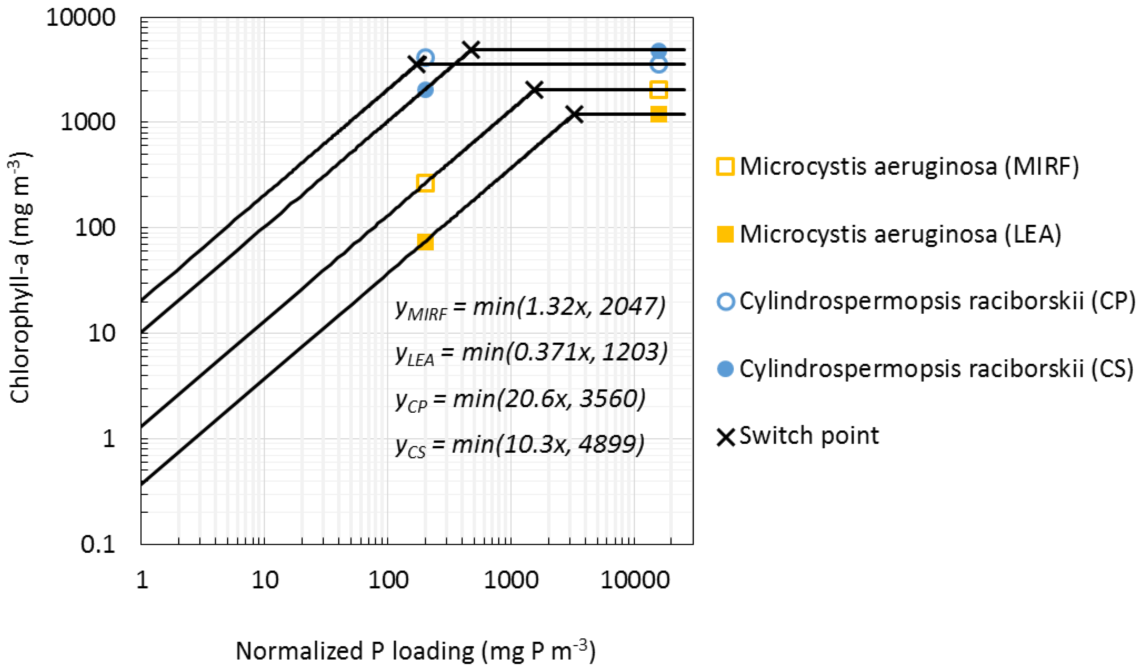


Figure 3.5 GPLake results for four strains of two phytoplankton species (*Microcystis aeruginosa* and *Cylindrospermopsis raciborskii*) in four Brasilian lakes. Codes refer to Marinho et al (2013). There are two measurements on each black line, one measurement is from a phosphorus limitation experiment and another measurement is from a light limitation experiment. The points shown by the black crosses show the position where the nutrient limitation switches to light limitation, which are calculated by Equation (3.5).

3.3.1.3 Parameterization of GPLake with model output

The result of the parameterization of GPLake with the output of PCLake is shown in Figure 3.6. The grey dashed line shows the PCLake results with the default setting, and the black dots show PCLake results in the same default settings except that aquatic vegetation was excluded. Furthermore, lake characteristics like dilution rate, depth, fetch, N:P ratio of nutrient loading and sediment type can be associated with the values of GPLake generic parameters. In Appendix 3.3 we present examples with different settings using PCLake. This comparison revealed clear positive impacts of fetch on the *Slope* while not impacting the *Plateau*. Lake depth was shown to strongly impact the *Plateau* of phytoplankton concentration, while not affecting the *Slope*. This is in line with the two scaling constants c_1 and c_2 of GPLake.

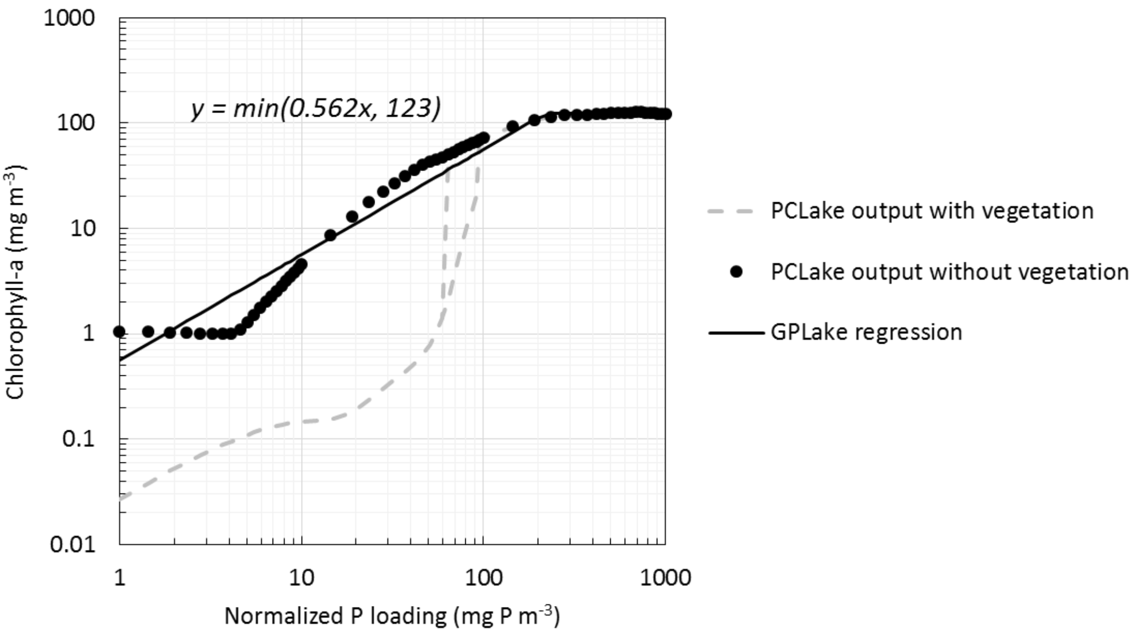


Figure 3.6 PCLake output and GPLake fit. The grey dashed line shows the results of PCLake under the default setting for a series of nutrient loading values ranging from oligotrophic to hypertrophic conditions, normalized nutrient loadings range from 1 to 1000 mg P m^{-3}, following the normalization method proposed by Vollenweider (Equation (3.9)) (Vollenweider, 1975; Jones et al., 1988). The black dots show the simulations with the same parameter setting as the default values, with the exception that aquatic vegetation is excluded. We calibrated the *Slope* and *Plateau* of GPLake with the results of the simulations excluding aquatic vegetation, because in GPLake vegetation is not considered.

3.3.1.4 Parameterizing GPLake combining the three sources of knowledge

Next, we brought together all values for the generic parameters of GPLake that we estimated from field data, lab data and model output as explained above. The result is a set of *Slopes* and *Plateaus* that are characteristic for each source of knowledge (Table 3.4). With these *Slopes* and *Plateaus*, we estimated the scaling constants c_1 and c_2 for each data set within the three knowledge sources. The differences between the resulting scaling constants might be attributed to different species or light conditions in the different systems. This difference can be used as an indicator of the uncertainty of GPLake (Figure 3.7). Averaging the scaling constants from the three knowledge sources resulted in a value of 115 day mg mg^{-1} for c_1 and 194 mg m^{-2} for c_2.

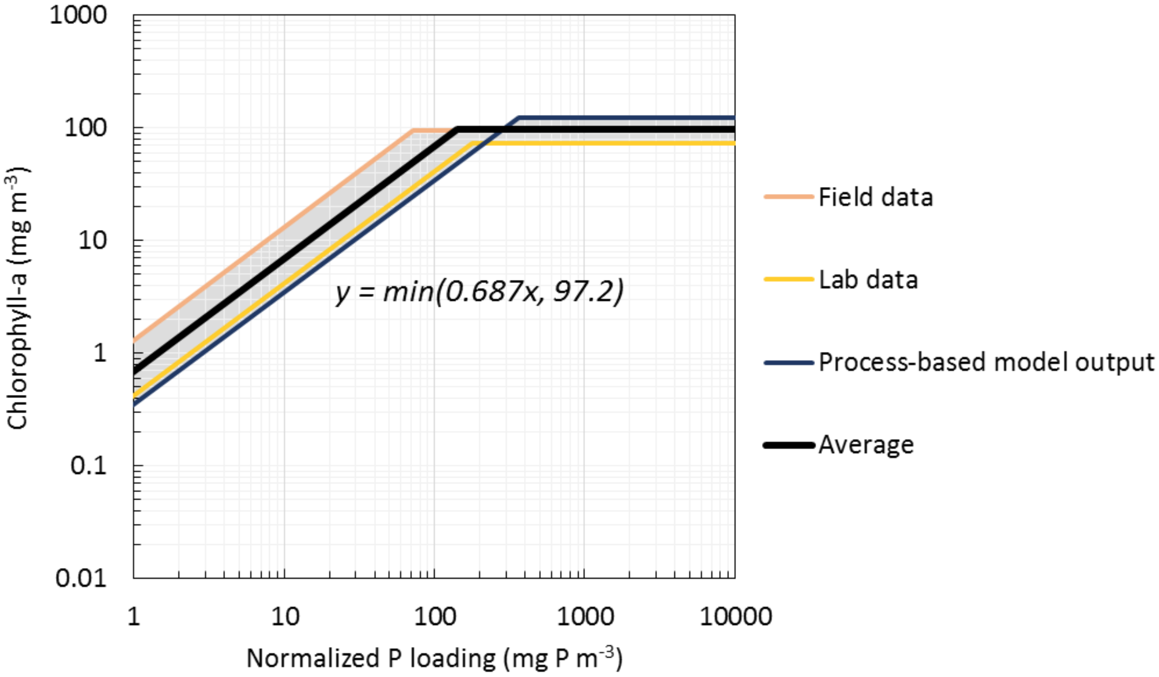


Figure 3.7 Graphical depiction of the GPLake parameters fitted on the basis of field data, lab data and model output and scaled for a hypothetical lake with 2 m depth and 0.006 day^{-1} dilution rate using Equation (3.10a-b) (see Table 3.5 for technical details and numerical values). The field data are representative for natural communities of phytoplankton species. The lab data are an average of the generic parameters of GPLake fitted for *Microcystis aeruginosa* and *Cylindrospermopsis raciborskii*. The process-based model output resembles an ensemble of functional types of green algae, diatoms and cyanobacteria. The black line shows the average of all the generic parameters of GPLake for the three approaches. Please note that the apparent visual similarity of the *Slope* parameter of GPLake is a result of the log-log scale. Differences in *Slopes* result in differences in intercept in the log-log plot shown here. The steepness of one of each of the lines in the log-log plot shown here reflects the fact that GPLake assumes a linear response of chl-a to nutrient loading in the nutrient-limited phase of the model (Figure 3.2).

3.3.2 Application of GPLake

For the application of GPLake the depth, dilution rate and nutrient load of the system are required. To showcase the application of GPLake, we added an appendix with a simple Excel GPLake tool to get a first approximation of the water quality of any lake system (see Appendix 3.5). Moreover, here we give a detailed example with background information on the application of GPLake to a hypothetical lake of 2 m depth and a dilution rate of 0.006 day^{-1}.

Table 3.4 Parameterization of GPLake scaling constants

Knowledge source	Data set	*Slope* (mg mg^{-1})	*Plateau* (mg m^{-3})	c_1 (day mg mg^{-1})	c_2 (mg m^{-2})
Field data	Vollenweider	0.235	25.3	343	253
	Janse	0.560	64.2	95.8	128
	Average			219[a]	191[a]
Model output	PCLake	0.562	123	56.2[a]	246[a]
Lab data	*MIRF*	1.32	2047	11.0	102
	LEA	0.371	1203	3.09	60.1
	CP	20.6	3560	172	178
	CS	10.3	4899	85.7	245
	Average			67.9[a]	146[a]
Overall average				115[b]	194[b]

[a] **These numbers are averaged to calculate the final value of the scaling constants.**

[b] **Final scaling constants used for the GPLake application.**

The application of GPLake is based on the scaling constants c_1 and c_2. The overall average of the scaling constants presented in Table 3.4 was used as default for a first approximation of the water quality. We used the different estimates of the scaling constants based on the three data sources to give an indication of the uncertainty (Table 3.5). With Equation (3.10a-b) we scaled the *Slopes* and *Plateaus* for our hypothetical lake (Table 3.5). Figure 3.7 shows a comparison for the resulting *Slopes* and *Plateaus*. Scaling the *Plateaus* to a specific system of a given depth and dilution rate results in the disappearance of the strong differences in GPLake *Plateaus* that we have previously observed among the different sources of knowledge (Table 3.4 vs Table 3.5). The physiological limitation, set by a more or less constant available light I_{in} for each of the systems, leads to this apparent constant upper boundary for phytoplankton concentration. Moreover, we also obtained *Slopes* of comparable degree for each of the data sources (Table 3.5). The slight differences between the GPLake *Slopes* (represented by different intercepts in the log-log plot of Figure 3.7) might be attributed to different sets of traits in the phytoplankton community assemblage in each system. Now, given the current nutrient load of the system as known by the lake manager, the water quality can be determined. For example, if the current nutrient load is 1 mg P m^{-2} day^{-1}, the normalized P-loading will be 49.8 mg P m^{-3} and the chl-a level approximated by GPLake will be 34.3 mg m^{-3} (numbers obtained by the GPLake tool, Appendix 3.5).

Table 3.5. GPLake parameterization for a hypothetical lake of 2 m depth and 0.006 day^{-1} dilution rate. Using the scaling constants c_1 and c_2 from Table 3.4 and Equation (3.10a-b) the generic parameters *Slope* and *Plateau* and the auxiliary parameter $R_{in,switch}$ are scaled.

	c_1 (day mg mg^{-1})	c_2 (mg m^{-2})	*Slope* (mg mg^{-1})	*Plateau* (mg m^{-3})	$R_{in,switch}$ (mg m^{-3})
Scaled field data	219	191	1.32	95.4	72.4
Scaled lab data	67.9	146	0.408	73.2	180
Scaled model output	56.2	246	0.337	123	365
Overall average	115	194	0.687	97.2	206

3.4 Discussion

3.4.1 Towards a generically parameterized model of lake eutrophication

Our aim with GPLake is to provide water quality managers with a model that is 1) as solid in its derivation from ecological theory as the Tilman nutrient competition and Huisman light competition models, 2) as versatile in its parameterization that it can be based on either field data, lab data or model output and 3) as simple in its application as the calibration lines provided by the linear regressions through the Vollenweider and Janse data sets. These three points reflect each of the three steps we went through: derivation, parameterization, and application. First, we achieved our first aim, by providing expressions (Equation (3.4a-b)) for how *Slope* and *Plateau* relate to the parameters of the models from Tilman, 1982 and Huisman et al., 1994; 1995; Huisman et al., 2002. We provided expressions for how *Slope* and *Plateau* scale with dilution rate and depth (Equation (3.10a-b)), respectively, thereby paving the way for the parametrization of GPLake from field-, lab- or model- systems that differ in depth and dilution rate to satisfy our second aim. This resulted in a parameterized model of lake eutrophication that has only two parameters: *Slope* and *Plateau*. Together these parameters form a simple expression (Equation (3.11)) by which a first estimate of chl-a as a function of the inflowing nutrient concentration can be obtained, thereby satisfying our last aim. With GPLake we thus have a model that is simple in its application. A full appreciation of the derivation of GPLake requires a certain level of familiarity with consumer-resource theory, while a full understanding of the parameterization of GPLake requires some basic mathematical and statistical skills. Application of GPLake, however, requires only a few calculations that can be performed by anyone with a basic knowledge of Excel (Appendix 3.5).

While we fully achieved each of our three aims, one could ask what the added value of GPLake is over the linear regressions through the Vollenweider and Janse data sets (Vollenweider, 1975; Jones et al., 1988), given that GPLake fits these data sets with a slightly higher unexplained variance for both data sets. We argue that indeed for those cases where extensive empirical knowledge on the system of interest is available, a statistical approach will most likely produce more accurate results than a mechanistic approach because the latter approach is more constrained in the type of functional relationships. However, data availability here relates to both the types of lakes as well as the range of nutrient loadings for which data are available. Therefore, statistical approaches such as Vollenweider's are bound to the calibration domain (Cuddington et al., 2013). In fact, our analysis shows that at low and high nutrient loadings the linear regressions on the Vollenweider respectively Janse data sets in log-log space are bound to fail because statistical approaches will lead to unrealistic chl-a to nutrient ratios at very low loadings and to unrealistic high chl-a levels when light limitation sets in. The mechanistic foundation of GPLake deals with both issues. But even within the range of nutrient loadings for which observations are available in the Vollenweider and Janse data sets one could question a one-to-one application of these data. Vollenweider's data were collected in the 1980s when lakes had a different loading history and where exposed to different climatic conditions compared to the current situation. Such differences might be captured by process-based models

(Cuddington et al., 2013) which can then serve as a source of data to parameterize GPLake. Or one might rely on GPLake parameters that are derived from lab experiments with the most dominant phytoplankton species that occur in a given lake.

3.4.2 Scientific significance of GPLake

This study addresses three basic scientific issues involved in understanding lake eutrophication through modelling. The first issue is whether empirical models, limited by their calibration domain, can be extended to apply to a wide variety of lakes (Janssen et al., 2019a). The second issue is whether theoretical models, parameterized with and tested against laboratory experiments, can be scaled up to make predictions regarding large ecological systems such as lakes (akin to Schindler, 1998). The third issue is whether complex process-based models can be scaled down in complexity (Murray, 2007; Kuiper et al., 2015) to a simple, transparent mathematical version that still captures the essential features of the complex model and, to a good approximation, the main predictions of that model. In this study we deal with those scientific issues by presenting the simple, transparent and flexible approach of GPLake, which links the three key sources on lake eutrophication (Figure 3.1, GPLake parameterization). By condensing the available sources of knowledge into two generic parameters, *Slope* and *Plateau*, GPLake creates synergy between the realism of the empirical approach, the scientific transparency of the theoretical approach and the flexibility in the application domain of the process-based approach.

GPLake shares its number of generic parameters with the power functions that are typically fitted to Vollenweider-type data sets (e.g., Vollenweider, 1975) and Nürnberg, 1984), but it does so through its link with theory, which gives a specific, mechanistically interpretable meaning to both the *Slope* and *Plateau*. The mechanistic foundation of the two generic parameters allows us to easily scale these parameters for different lakes and their specific depths and dilution rates. Like GPLake, models applying the process-based approach such as PCLake are themselves based on a combination of first principles, lab-derived and heuristic functions and parameters, but the two models differ enormously in the number of parameters (GPLake 2, PCLake > 300). This makes the application of GPLake simpler than that of PCLake.

GPLake is able to link knowledge from three approaches by describing the relationship between nutrient loading and phytoplankton concentration at equilibrium that is shared by all three approaches. This relationship addresses one of the most substantial questions to eutrophication studies: what is the maximum equilibrium phytoplankton concentration that can be produced given a certain nutrient loading (Prairie et al., 1989; Smith et al., 1999)? The three approaches have complementary strengths in answering this question and GPLake combines these strengths and shows their compatibility. The empirical approach addresses this question by deriving statistical relationships between nutrients and chl-a based on a large number of lakes (e.g., Dillon et al., 1974; Vollenweider, 1975). Importantly, the averaging and steady-state assumptions underlying these relationships (Brett et al., 2008) are adopted in GPLake to derive realistic values of the model's generic parameters. In comparison, the theoretical approach addresses this question by a prediction based on first principles. These first principles provide mechanistic interpretations of how much nutrients can be consumed by phytoplankton, depending on the nutrient or light supply (Tilman, 1982; Tilman et al., 1982; Huisman et al., 1994). GPLake scales these transparent results from the theoretical approach to real systems found in the field. Finally, the process-based approach addresses this question by applying the accumulated knowledge of biogeochemical processes in ecosystems. The process-based approach has the flexibility to describe a wide variety of lakes through different parameter combinations (Janssen et al., 2019a). By simplifying the output of the process-based model PCLake using GPLake, we revealed how the different lake characteristics affect the *Slope* and *Plateau* (Appendix 3.3).

The effectiveness of GPLake is shown by the consistency between GPLake and field data sets (Figure 3.4), with comparable explanatory power (Table 3.3). Moreover, once scaled to a system of comparable depth and dilution rate, GPLake obtained similar *Slope* and *Plateau* parameters independent of whether the model was parameterized based on field data, lab data or model output (Table 3.5 and Figure 3.7), allowing us to increase our understanding of lake ecosystems through multiple approaches. First, GPLake considers the underlying mechanisms, allowing a better interpretation of differences in shallow (Janse) and deep (Vollenweider) lake data sets (section 3.1.1). Second, laboratory studies provide lab data for the parameterization of GPLake that represent accurate measurements of phytoplankton growth under controlled conditions (section 3.1.2, (Huisman et al., 2002)). Third, existing process-based models provide model output to build a database that associates lake characteristics to GPLake parameters to serve eutrophication management. Lake managers can estimate the parameter values according to their lake types (e.g., sand or peat lake) from that database and build specific GPLake models for their lakes. We have shown that all three approaches, when scaled by depth and dilution rate, showed comparable outcomes, implying a wide application domain of GPLake.

3.4.3 Societal significance of GPLake

We were motivated to develop GPLake by the practical demands of water quality management; therefore, simplicity in both inputs as well as model interpretation is key. The application goal of GPLake is to diagnose the trophic status of lakes using simple inputs. The two generic GPLake parameters, *Slope* and *Plateau*, contain all the information needed to apply GPLake in addition to the depth, dilution rate and nutrient loading of the system under study. Similar to general practitioners giving a first diagnosis to a patient, GPLake uses these two generic parameters as first diagnostic indicators of lake ecosystem health. This diagnosis includes whether the system is in the nutrient or the light limitation phase. As an example, we showed a hypothetical case study with a lake of 2 m depth and a 0.006 day^{-1} dilution rate. For this lake the field data, lab data and model output were linked and showed a similar result (Table 3.5 and Figure 3.7). The results gained by Figure 3.7 show that the advantage of GPLake lies in that lake managers have a simple tool for which only depth, dilution rate and nutrient loading are needed to obtain a first indication of the chl-a concentration. Moreover, with some basic mathematical skills managers can make use of simple lab studies to parameterize GPLake for their specific situation (for details see Appendix 3.6). Thereby, it offers a straightforward and cost effective way (via a lab study) to assess the needed nutrient reduction effort to reach chl-a targets. Moreover, it allows managers to make first-order assessments of measures such as decreasing residence time (c.f. increasing dilution rate) and changing depth profiles. This is possible because GPLake provides mechanistic information for lakes, and thus is not constrained by the range of lakes for which data are available. Therefore, it enables managers to make predictions for lakes not represented by existing regression models, such as those for the Vollenweider data, with only data for depth and residence time as a requirement. Finally, GPLake provides information about whether the lake is light-limited or nutrient-limited. This additional information, which is out of the scope of the Vollenweider model, can provide information to lake managers on the limiting resource in their lake. Using GPLake, a lake manager can identify 1) the expected current phytoplankton concentration (Schindler, 1978), 2) risk of blooms with increasing nutrient loads (Carvalho et al., 2011) and 3) the reduction targets to reach a desirable level of phytoplankton concentration (i.e., Jeppesen et al., 2005). Please note, however, that while phytoplankton concentration may stagnate in the light limitation phase (*Plateau*), the toxin production by the phytoplankton community may change strongly along a gradient of nutrient supply (Paerl, 2006; Van de Waal et al., 2014). Hence, we envision that GPLake can act as a ‘general practitioner model’ that gives a first diagnosis of the response of phytoplankton to lake eutrophication and from there paves the way for more specialized studies with empirical, theoretical or process-based approaches. Or, alternatively, the model can be used for lakes of which data are scarce but estimates of depth and residence time are available (Messager et al., 2016b).

3.4.4 Limitations of GPLake

While we have shown the general applicability of GPLake as a practical management tool, several limitations of GPLake need to be considered. An obvious limitation of the GPLake model is the equilibrium assumption. Consequently, GPLake is suitable as long-term prediction tool for lakes but is not suitable as a tool to predict daily phytoplankton bloom formation. The assumption that R_1^* is zero suggests that in the nutrient limitation phase the phytoplankton in the lake can take up all the nutrients in the lake system independent of the nutrient concentration itself. This assumption may not apply to highly oligotrophic lakes that have little nutrient loading. Yet these highly oligotrophic lakes are rare, especially in our contemporary world where many lakes are heavily eutrophied (Rigler, 1956; Paerl et al., 2009). Besides, GPLake captures only the relationship between nutrient loading and phytoplankton concentration, thereby ignoring other primary producers like aquatic vegetation. Consequently, GPLake will have difficulties when applied to lakes with significant aquatic vegetation growth. A further limitation is that only P and light are considered as limiting factors in GPLake, yet N also plays a role in the eutrophication of lakes (Lewis Jr et al., 2008; Conley et al., 2009). Based on the study by Smith, 1982, we expect that the pattern with a *Slope* and *Plateau* shown by GPLake can also be found in systems that differ in limitation factors: for example, a system first limited by P and later by N, first limited by N and later by light, or first limited by N and later by P. Concerning the light limitation phase, GPLake ignores the impact of background light extinction, for instance by humic substances, that may lead to a lower phytoplankton concentration. The focus of this study on an idealized case of nutrient and light limitation effects on phytoplankton development will not answer all questions of ecologists and managers. However, it will facilitate comparison of general patterns across many lakes and reservoirs. Moreover, each of the mentioned limitations will necessarily lead to lower phytoplankton concentrations than those predicted by GPLake. As such, GPLake can be seen as a worst case predictor of phytoplankton concentration in response to eutrophication.

3.4.5 Future directions for GPLake

GPLake provides a common language to link data obtained from empirical, theoretical and process-based approaches. Hence it is possible to use GPLake as a ‘meeting point’ (Figure 3.1) that connects the knowledge captured by the three approaches and that facilitates benefiting from their complementarity (Figure 3.7). In the future, we foresee that water quality is assessed by a further and deeper integration of field-, lab- and model-based knowledge (i.e., deeper than identified by Robson, 2014), and we propose that GPLake provides a mechanism to do so. We foresee the build-up of a library of GPLake *Slopes* and *Plateau* parameter values from more lab data, field data and model output (see Robson et al., 2018), which would allow one to inspect the average and variance in these generic parameters and the scaling constants. Finally, the values of *Slope* and *Plateau* can be further studied by directly using the lake biogeochemical characteristics from Equation (3.4a-b) from specific lakes to compare with the calibration result.

3.5 Conclusions

Eutrophication is an ongoing challenge in the Anthropocene that is caused by excessive nutrients originating from human activities. In addressing these challenges, many studies have provided rich and diverse knowledge on lake eutrophication. By developing GPLake we have taken up the scientific and societal challenge to link three sources of knowledge: field, lab and model-based. Linking this knowledge contributes to both scientific understanding and lake management. By connecting different approaches that are each characterized by their own scale and complexity, GPLake provides a common language for lake managers. GPLake is able to indicate the limiting factors of lakes and provides lake managers with a cost-effective way to quickly gain insight into expected chl-a levels for a wide range of nutrient loads. Additionally, GPLake assists managers in making a first-order assessment of measures such as increasing residence time or changing depth, and allows them to assess the amount of effort needed for nutrient load reduction to meet their water quality standards. As such, GPLake can be regarded as a versatile and cost-effective tool to estimate the trophic state of lakes and to explore solutions to eutrophication issues.

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Chapter 4

A Generically Parameterized model of Lake eutrophication: the impact of Stoichiometric ratios and constraints on the abundance of natural communities of phytoplankton (GPLake-S)

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Abstract

Management of water quality to avoid excessive blooms of phytoplankton and their negative impacts on desired ecosystem services often requires eutrophication management. It is increasingly clear that anthropogenic inputs of both phosphorus (P) and nitrogen (N) need to be considered when assessing the impacts of nutrients on phytoplankton abundance. There are two scientific domains that can provide insight in the excessive production of phytoplankton in response to nutrient loading: empirical eutrophication studies and ecological resource competition theory. Empirical eutrophication studies are generally aimed at managing excessive phytoplankton abundance in aquatic ecosystems without concerning underlying mechanisms of species competition for resources, while ecological resource competition theory tends to focus on the outcomes of competition in terms of species coexistence and on resource depletion, rather than on the resulting abundance of the community as a whole. Here, we argue that combining the ecosystem level predictions in terms of chlorophyll-*a* concentrations under changing nutrient supply from empirical eutrophication studies with a mechanistic understanding of how the balance of energy in the form of light and multiple nutrients shape species interactions of phytoplankton communities according to ecological resource competition theory is key to predict and manage eutrophication. To this end we present GPLake-S, a mechanistic model rooted in ecological resource competition theory with a limited set of parameters and able to make predictions of chlorophyll-*a* to nutrient relationships for phytoplankton communities under N, P, N+P colimitation and light limitation conditions. GPLake-S offers a simple yet mechanistically based tool to make first order predictions of nutrient thresholds relevant for water management and policy.

4.1 Introduction

Eutrophication is a hallmark of the Anthropocene. All over the world increased anthropogenic input of phosphorus (P) and nitrogen (N) to aquatic ecosystems causes water quality problems (Conley et al., 2009; Thornton et al., 2013). Eutrophication threatens drinking water supply, fisheries, bathing water and the aesthetic value of natural and recreational water bodies (Paerl, 1988; Carpenter et al., 1998). These problems are due to large amounts of phytoplankton which water quality managers generally express in terms of chlorophyll-*a* (hereafter shortened to chl-*a*) levels. The excessive production of phytoplankton can outcompete plants through shading (Scheffer et al., 1993), cause oxygen depletion (Hallegraeff, 2003) and some phytoplankton species produce toxins that are harmful to humans and animals (Carmichael, 2001; Codd et al., 2005). Excessive phytoplankton abundance is strongly driven by P- and N-loading from - among others - fertilizer and sewage water inputs into aquatic ecosystems (Conley et al., 2009). Nutrient load reduction seems the most fundamental solution to mitigate eutrophication problems (Jeppesen et al., 2007a). However, careful estimation of what nutrients are limiting phytoplankton abundance, and to what amount nutrient inputs should be reduced, are required because management efforts are costly and will have socio-economic implications (Janssen et al., 2019a; Janssen et al., 2020). Specifically, an important question of eutrophication management is to what extent P- and N-loadings should be reduced to meet water quality standards that are acceptable to society and prescribed by legislation (Directive, 2000).

There are two scientific domains that provide insight in the excessive production of phytoplankton in response to nutrient loading: empirical eutrophication studies (Vollenweider, 1968; Dillon et al., 1974; Schindler, 1974; Nürnberg, 1984) and ecological resource competition theory (Tilman, 1982; Huisman et al., 1994). Empirical eutrophication studies aim to reveal which levels of phytoplankton abundance can be expected in natural systems under a given level of nutrient loading and how acceptable levels can be ensured through water quality management. One of the most widely applied eutrophication models is developed by Vollenweider (1968). It is an empirical model that describes the relationship between P-loading and chl-*a* concentrations through statistical analysis of data from several hundred lakes worldwide. Later on, others expanded Vollenweider's seminal approach to lakes with different characteristics, whilst maintaining the same model structure and goal (Kimmel et al., 1984; Nürnberg, 1984; Lijklema et al., 1989). Based on the seminal work of Schindler (Schindler, 1974), most of these studies focus on the relationship between P and chl-*a* (Dillon et al., 1974; Canfield Jr et al., 1981; Wagner et al., 2011) and ignore other limitations despite the fact that these have shown to be equally important (Conley et al., 2009; Paerl et al., 2009). On the other hand, ecological resource competition theory focuses on the mechanistic underpinning of species coexistence under variable ratios of nutrient supply (Tilman, 1982) and incident light (Huisman et al., 1994).

While the scientific domains of empirical eutrophication studies and ecological resource competition theory both address the relation between nutrients, light and phytoplankton abundance, they are not seamlessly linked. Empirical eutrophication studies are generally aimed at managing excessive phytoplankton abundance in aquatic ecosystems without concerning underlying mechanisms of species competition for resources (Vollenweider, 1968; Smith et al., 2009). Moreover, empirical eutrophication studies have largely ignored relevant nutrients other than P (e.g. the role of N-limitation in Conley et al., 2009; Paerl et al., 2009). Ecological resource competition theory tends to focus on the outcomes of competition in terms of species coexistence and on resource depletion, rather than on the resulting abundance of the community as a whole (Tilman, 1982; Huisman et al., 1994), and offers mechanistic insights in the role of both P and N supply ratios for phytoplankton consumer-resource dynamics, but mostly stays short of making predictions of total chl-*a* concentrations under natural conditions. Here, we strive to combine the ecosystem level predictions of chl-*a* concentrations under changing nutrient supply from empirical eutrophication studies with a mechanistically understanding of how the balance of energy in the form of light and multiple nutrients shape species interactions of phytoplankton communities according to ecological resource competition theory.

In this paper we present the GPLake-S model, where GPLake stands for Generically Parameterized Lake model, and S stands for Stoichiometry. The philosophy of GPLake (Chang et al., 2019b) and GPLake-S (this study) is to provide simple but mechanistic tools that can give a first estimation of chl-*a* level and limiting factor in eutrophication management for a wide range of lake characteristics (Chang et al., 2019b). GPLake-S captures the relationship between P- and N-loadings and chl-*a* concentrations of phytoplankton communities in surface waters. Specifically, we aim for developing a model that gives predictions of chl-*a* concentrations in natural systems under a wide range of P- and N-loadings based on first principles of ecological resource competition theory (Tilman, 1982). Whereas the original GPLake model focuses on the shift from a single limiting nutrient to light limitation in a gradient of nutrient loading (Chang et al., 2019b), the expanded model GPLake-S presented here describes the relationship between multiple limiting nutrients and average chl-*a* concentration at equilibrium for natural communities of phytoplankton species. A key assumption of GPLake-S is that the species in natural communities of phytoplankton cover a diverse spectrum of stoichiometric demands that allows the community to adjust to a range of nutrient supply ratios.

To develop GPLake-S we address the following research questions: 1) What are the first principles that determine the relation between phytoplankton abundance and the loading of two limiting nutrients according to ecological resource competition theory; 2) How can we capture the stoichiometric variability in natural communities of phytoplankton for two limiting nutrients in ecological resource competition models and what assumptions do we make in doing so?; 3) Which types of resource limitations does GPLake-S comprise and what are the equilibria for chl-a, P and N for each type?; 4) How can we find generic parameters for GPLake-S on the basis of field, lab and model data?

4.2 Methods

4.2.1 Theoretical background for GPLake-S

We base our model on explicit ecological resource competition theory sensu (Tilman, 1982). For the case of a single consumer W_1 growing with Michaelis-Menten kinetics (Michaelis et al., 1913; Cornish-Bowden, 2015) on a single resource R_1 with chemostat dynamics (this model is further referred to as the 1R1W TM model) we get

$$\frac{dR_1}{dt} = Net\ supply\ of\ R_1 - Consumption\ of\ R_1\ by\ W_1$$

$$= D\left(R_{1,in} - R_1\right) - c_{R_1,W_1} p_{W_1,max}\left(\frac{R_1}{R_1 + H_{R_1,W_1}}\right) W_1 \tag{4.1}$$

$$\frac{dW_1}{dt} = Production\ of\ W_1 - Loss\ of\ W_1$$

$$= p_{W_1,max}\left(\frac{R_1}{R_1 + H_{R_1,W_1}}\right) W_1 - l_{W_1} W_1 \tag{4.2}$$

where D is the dilution rate, $R_{1,in}$ the inflowing nutrient concentration, $c_{R1,W1}$ is the stoichiometric constant describing the amount of resource per unit of consumer, $p_{W1,max}$ is the maximum consumer specific growth rate, $H_{R1,W1}$ is the resource concentration at which the realized specific growth equals half the maximum specific growth rate and l_{W1} is the specific loss rate of the consumer.

For this system to be in equilibrium the mass balance equation of the resource

$$D\left(R_{1,in} - R^*_{1,W_1}\right) = l_{W_1} c_{R_1,W_1} W^*_1 \tag{4.3}$$

should be fulfilled (Figure 4.1). Here, the left hand term reflects the amount of resources that flows into the system minus what flows out, whereas the right hand term reflects the loss rate of the consumers. This fundamental equation forms the basis of the nutrient limited phase of GPLake (Chang et al., 2019b). An important assumption in GPLake is that for realistic parameterizations of phytoplankton growing under P-limitation $R^*_{1,W1}$ can be ignored because it hardly affects the equilibrium concentration W^*_1 thereby simplifying the above mass balance to

$$DR_{1,in} = l_{W_1} c_{R_1,W_1} W_1^* \tag{4.4}$$

and hence resulting in an explicit formula for the equilibrium phytoplankton concentration under nutrient limitation

$$W_1^* = \frac{D}{l_{W_1}} \frac{R_{1,in}}{c_{R_1,W_1}} \tag{4.5}$$

Please note that the equilibrium density of consumers is proportional not only to the stoichiometric constant $c_{R1,W1}$ but also to the ratio of the dilution rate D and the specific consumer loss rate l_{W1}. Hence, the higher the retention of consumers in the system, the lower the abundance of the consumers is. Under chemostat conditions with D equal to l_{W1} this further simplifies to

$$W_1^* = \frac{R_{1,in}}{c_{R_1,W_1}} \tag{4.6}$$

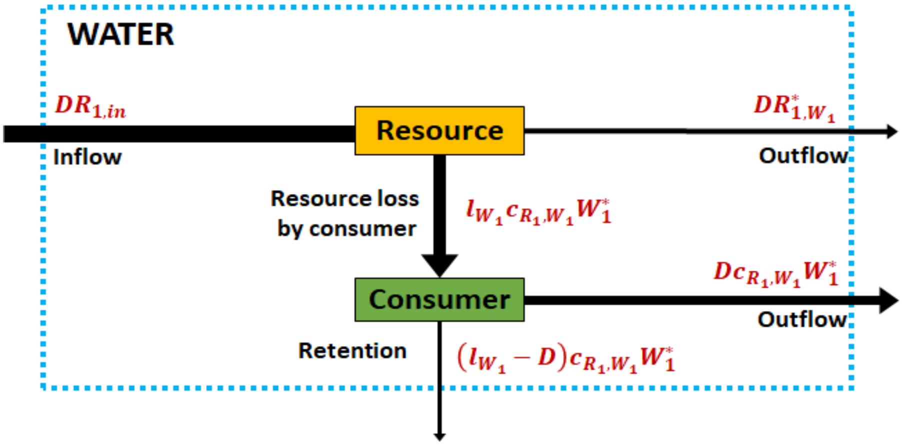

Figure 4.1 Graphical depiction of the fundamental mass balance underlying GPLake (Chang et al., 2019b) and GPLake-S (this study). In equilibrium, the inflow of resources (in this study P or N) should match the loss of resources through outflow as dissolved resources and the resources in the outflowing consumers (in this study phytoplankton) as well as the loss of resources through retention of consumers. Text in black indicates the compartments and processes included in both models and text in red gives the mathematical process formulations.

When expanded to two consumers *W₁* and *W₂* competing for two resources *R₁* and *R₂* according to Liebig's law of the minimum the resulting model becomes

$$\begin{aligned}\frac{dR_1}{dt} &= Net\ supply\ of\ R_1 - Consumption\ of\ R_1\ by\ W_1 \\ &\qquad - Consumption\ of\ R_1\ by\ W_2 \\ &= D\left(R_{1,in} - R_1\right) - c_{R_1,W_1} p_{W_1} W_1 - c_{R_1,W_2} p_{W_2} W_2 \end{aligned} \tag{4.7}$$

$$\begin{aligned}\frac{dR_2}{dt} &= Net\ supply\ of\ R_2 - Consumption\ of\ R_2\ by\ W_1 \\ &\qquad - Consumption\ of\ R_2\ by\ W_2 \\ &= D\left(R_{2,in} - R_2\right) - c_{R_2,W_1} p_{W_1} W_1 - c_{R_2,W_2} p_{W_2} W_2 \end{aligned} \tag{4.8}$$

with *dR₁/dt* and *dR₂/dt* describing the change in resource 1 and resource 2, respectively. Moreover, we get

$$\begin{aligned}\frac{dW_1}{dt} &= Production\ of\ W_1 - Loss\ of\ W_1 \\ &= p_{W_1} W_1 - l_{W_1} W_1 \end{aligned} \tag{4.9}$$

$$\begin{aligned}\frac{dW_2}{dt} &= Production\ of\ W_2 - Loss\ of\ W_2 \\ &= p_{W_2} W_2 - l_{W_2} W_2 \end{aligned} \tag{4.10}$$

with *dW₁/dt* and *dW₂/dt* describing the change in consumer 1 and consumer 2, respectively. In both sets of equations

$$p_{W_1} = min\left(p_{W_1,max}\left(\frac{R_1}{R_1 + H_{R_1,W_1}}\right), p_{W_1,max}\left(\frac{R_2}{R_2 + H_{R_2,W_1}}\right)\right) \tag{4.11}$$

$$p_{W_2} = min\left(p_{W_2,max}\left(\frac{R_1}{R_1 + H_{R_1,W_2}}\right), p_{W_2,max}\left(\frac{R_2}{R_2 + H_{R_2,W_2}}\right)\right) \tag{4.12}$$

with p_{w1} and p_{w2} respectively being the realized specific growth rate of consumers 1 and 2. This model has similar parameters as the 1R1W TM model and will be further referred to as the 2R2W TM model.

For the 2R2W TM model to be in equilibrium the mass balance equations of both resources

$$D\left(R_{1,in} - R_1^*\right) = l_{W_1} c_{R_1,W_1} W_1 + l_{W_2} c_{R_1,W_2} W_2 \tag{4.13}$$

$$D\left(R_{2,in} - R_2^*\right) = l_{W_1} c_{R_2,W_1} W_1 + l_{W_2} c_{R_2,W_2} W_2 \tag{4.14}$$

should be fulfilled. A striking and well known outcome of the 2R2W TM model is that the relative magnitude of the single consumer single resource equilibrium values $R^*_{1,W1}$, $R^*_{1,W2}$, $R^*_{2,W1}$ and $R^*_{2,W2}$, the supply concentrations of nutrients $R_{1,in}$ and $R_{2,in}$ and the ratio the stoichiometric constants $c_{R2,W1}/c_{R1,W1}$ and $c_{R2,W2}/c_{R1,W2}$ together determine the outcome of the competition between the W_1 and W_2 for R_1 and R_2 . See Figure 4.2 for the configuration we study here and Appendix 4.1 for mathematical and graphical expressions of all four possible configurations.

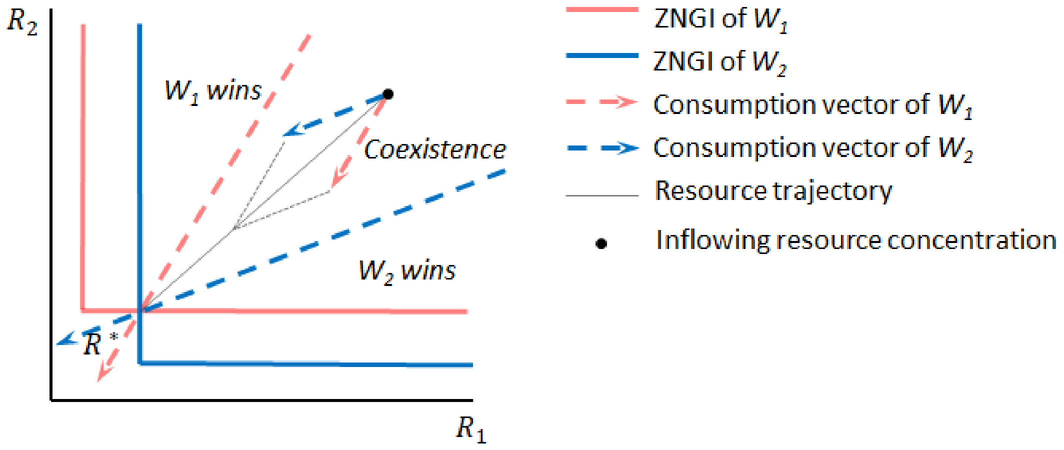

Figure 4.2 A graphical representation of Tilman's 2R2W resource competition model. The pink solid lines denote the zero net growth isoclines (ZNGIs) for consumer W_1 and the blue solid lines denote the ZNGIs for consumer W_2. The pink dashed arrows denote the ratio of the stoichiometric constants of W_1, i.e. $c_{R2,W1}/c_{R1,W1}$; the blue dashed arrows denote the ratio of the stoichiometric constants of W_2, i.e. $c_{R2,W2}/c_{R1,W2}$.; the black dot denotes resource supply concentrations $R_{1,in}$ and $R_{2,in}$; the black text denotes the outcome of competition given the position of resource supply concentration of nutrients. In the example shown here, intraspecific competition is stronger than interspecific competition because each consumer requires more of the nutrient for which it is the weaker competitor. This allows for coexistence between both consumers, given that the nutrient ratio supply is intermediate to the ratios of nutrient uptake of both consumers. This figure is adapted from (Tilman, 1982).

4.2.2 Applying competition theory to natural communities

In this study we focus on natural communities of phytoplankton growing under P and N limitation. This calls for a version of Tilman's resource competition model with a large number of *n* consumers W_i competing for two resources here denoted as the 2RnW TM model. The basic equations for this model are

$$\frac{dR_1}{dt} = Net\ supply\ of\ R_1 - Sum\ of\ consumption\ of\ R_1\ by\ W_i$$

$$= D\left(R_{1,in} - R_1\right) - \sum_i c_{R_1,W_i} p_{W_i} W_i \tag{4.15}$$

$$\frac{dR_2}{dt} = Net\ supply\ of\ R_2 - Sum\ of\ consumption\ of\ R_2\ by\ W_i$$

$$= D\left(R_{2,in} - R_2\right) - \sum_i c_{R_2,W_i} p_{W_i} W_i \tag{4.16}$$

$$\frac{dW_i}{dt} = Production\ of\ W_i - Loss\ of\ W_i$$

$$= p_{W_i} W_i - l_{W_i} W_i \tag{4.17}$$

$$\mu_{W_i} = min\left(p_{W_i,max}\left(\frac{R_1}{R_1 + H_{R_1,W_i}}\right), p_{W_i,max}\left(\frac{R_2}{R_2 + H_{R_2,W_i}}\right)\right) \tag{4.18}$$

For the 2RnW TM model system to be in equilibrium the mass balance equations of both resources

$$D\left(R_{1,in} - R_1^*\right) = \sum_i l_{W_i} c_{R_1,W_i} W_i \tag{4.19}$$

$$D\left(R_{2,in} - R_2^*\right) = \sum_i l_{W_i} c_{R_2,W_i} W_i \tag{4.20}$$

should be fulfilled. Obviously, there will be constraints on the maximum and minimum values of the stoichiometric constants in the community. Following Danger et al., 2008 we refer to the consumer with the highest value of $c_{R2,Wi} / c_{R1,Wi}$ as consumer W_α and the consumer with the lowest value of $c_{R2,Wi} / c_{R1,Wi}$ as consumer W_β and hence for any consumer W_i in the community it should hold that $c_{R_2,W_\alpha}/c_{R_1,W_\alpha} \geq c_{R_2,W_i}/c_{R_1,W_i} \geq c_{R_2,W_\beta}/c_{R_1,W_\beta}$. Along comparable lines of reasoning as with the 2R2W TM model, the outcome of the competition between the community of consumers W_α, …, W_β for two resources R_1 and R_2 in the 2RnW TM model is determined by the relative magnitude of the single consumer single resource equilibrium values $R^*_{1,Wi}$ and $R^*_{2,Wi}$, the supply concentrations of nutrients $R_{1,in}$ and $R_{2,in}$ and the stoichiometric constants $c_{R1,Wi}$, and $c_{R2,Wi}$.

To implement the 2RnW model we need to parameterize it for each of the species in the community. We did so by repeatedly defining new consumers with intermediate nutrients requirements through geometric interpolation. To exemplify this for the first step from 2 to 3 consumers we defined

$$c_{R_1,W_{intermediate}} = \sqrt{c_{R_1,W_\alpha} c_{R_1,W_\beta}} \qquad (4.21)$$

$$c_{R_2,W_{intermediate}} = \sqrt{c_{R_2,W_\alpha} c_{R_2,W_\beta}} \qquad (4.22)$$

where W_α and W_β represent the two species with the most extreme ratio of the stoichiometric constants and $W_{intermediate}$ represents the species that has an geometrically averaged value of consumption vector. From there we proceeded to define 5 consumers, and finally 9 consumers assuming that a further step to 17 consumers and beyond would yield little additional information. To concentrate our analysis on those species that potentially can coexist pairwise with the other species in the community - given that the ratio at which both resources are supplied to the system is intermediate to the requirements of that specific couple of consumers - we made the following assumptions on the $R^*_{1,Wi}$ and $R^*_{2,Wi}$ of each consumer such that

$$R^*_{2,W_i}/R^*_{1,W_i} = c_{R_2,W_i}/c_{R_1,W_i} \qquad (4.23)$$

and that

$$R^*_{1,W_i}R^*_{2,W_i} = C_{R^*} \qquad (4.24)$$

The resulting 2R9W TM model is illustrated in Figure 4.3.

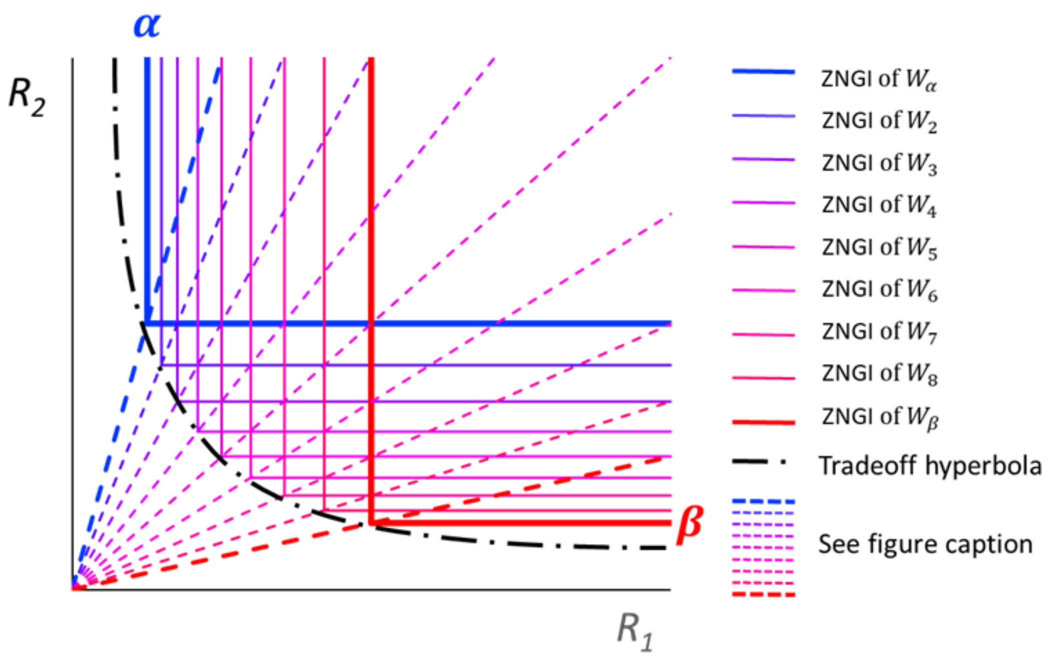

Figure 4.3 Expansion of the Tilman's model from 2R2W to 2RnW, illustrated for nine species (2R9W). Note that in this graph each of the depicted consumers W_i, has a potential resource depletion ($R^*_{1,Wi}$, $R^*_{2,Wi}$) that allows it to coexist with any of the other consumers given a suitable nutrient supply ratio. The consumers in the community with the most extreme resource uptake ratios are identified as W_α and W_β. The colored solid lines from blue to red are ZNGIs of the nine species. The colored dashed lines represent the ratios of the stoichiometric constants of these species $c_{R2,Wi}/c_{R1,Wi}$ as well as the ratios of their minimum resource concentration requirements $R^*_{2,Wi}/R^*_{1,Wi}$. The intersections of the ZNGIs of each species together form a hyperbola that obbeys of our assumption that $R^*_{1,Wi}\ R^*_{2,Wi} = C_{R^*}$. We call this hyperbola the "tradeoff hyperbola" because it represents the trade-off between the competitiveness for different nutrients of the species in the community.

4.2.3 Developing a model for natural communities of phytoplankton

While the above described community resource competition model is of a general nature and well-rooted in ecological theory, in this study we specifically apply it to natural communities of phytoplankton competing for phosphorus and nitrogen in the context of empirical eutrophication studies and call the resulting model GPLake-S. From here on we therefore refer to R_1 and R_2 as P and N, respectively. In a first step towards a practical model structure we examined the required model complexity in terms of the number of species (n) for a 2RnW model to capture the abundance of phytoplankton in terms of chl-*a* concentration along a nutrient supply ratio gradient (N_{in}/P_{in} from zero to infinity) properly, given our assumptions on the characteristics of the intermediate species. To do so we compared the analytical solution of chl-a concentrations along a nutrient supply ratio gradient for an infinite number of species with model calculations of 2, 3, 5 and 9 consumer models, called the 2R2W, 2R3W, 2R5W and 2R9W TM models, respectively. In a second step we parameterized the GPLake-S model. Continuing the strategy employed in GPLake (Chang et al., 2019b), we generically parameterized GPLake-S for reasonable ranges of stoichiometric constants of natural communities of phytoplankton on the basis of field data, lab data and model data.

4.3 Results

4.3.1 Choosing the number of species in GPLake-S

First, we studied the impact of varying the number of species to represent a natural community of phytoplankton in GPLake-S given our assumptions on defining intermediate species by analysing a number of TM models of increasing species complexity. Specifically, we carried out analyses with the 2R2W, 2R3W, 2R5W and 2R9W TM model along a gradient of inflowing nutrient concentrations P_{in} and N_{in} that can be described by

$$10P_{in} + N_{in} = 2000 \tag{4.25}$$

with $P_{in} \geq 0$ and $N_{in} \geq 0$ expressed in mg P m^{-3} and mg N m^{-3}, respectively. For the parameter settings used in this analysis see Appendix 4.2. The resulting abundance of the species and the total calculated chl-a concentration for the 2R2W TM model shows three zones along a nutrient supply ratio gradient: a linear response of chl-a concentration to the supply of P under P-limitation, a plateau with a gradual replacement of species W_α by species W_β and finally, a linear response to the supply of N under N-limitation (Figure 4.4a). In the 2R3W TM model, this plateau is replaced by a linear increase in chl-a concentration as species W_α is replaced by the intermediate species W_μ under colimitation by P and N and a linear decrease to as species W_μ is replaced by species W_β, again under colimitation (Figure 4.4b). Further splitting the community in 5 and 9 species (Figure 4.4c and d, respectively) gradually refines the zone of colimitation into a concave unimodal curve with a maximum chl-*a* concentration in case of a monoculture of the species W_{μ} with the intermediate nutrient requirements of the community. We obtained the curve for n goes to infinity under colimitation by calculating the abundance of the optimal species W^{*}_{i} (i.e. the species for which $c_{N,Wi}$ / $c_{P,Wi}$ = N_{in} / P_{in} with the additional constraint that $c_{P,W\alpha}\, c_{N,W\alpha} = c_{P,Wi}\, c_{N,Wi} = c_{P,W\beta}\, c_{N,W\beta}$) under P-limitation

$$200 > P_{in} > 0 \tag{4.26}$$

$$N_{in} = 2000 - 10\, P_{in} \tag{4.27}$$

$$c_{P,W_i} = \sqrt{\left(c_{P,W_\alpha} c_{N,W_\alpha}\right)(P_{in}/N_{in})} \tag{4.28}$$

$$W_i^* = \frac{P_{in}}{c_{P,W_i}} \tag{4.29}$$

or we could equally have used N limitation

$$0 < N_{in} < 2000 \tag{4.30}$$

$$P_{in} = 200 - \; N_{in}/10 \tag{4.31}$$

$$c_{N,W_i} = \sqrt{\left(c_{P,W_\alpha} c_{N,W_\alpha}\right)(N_{in}/P_{in})} \tag{4.32}$$

$$W_i^* = \frac{N_{in}}{c_{N,W_i}} \tag{4.33}$$

resulting the same values for W^{*}_{i} in the zone of colimitation. Compared with the 2RnW TM model, the 2R2W, 2R3W, 2R5W and 2R9W TM models show an average deviation of 11.5, 3.2, 0.9 and 0.3% from the algebraic solution, respectively. On the basis of these analyses, we consider the 2R3W TM model with species W_{α}, W_{μ} and W_{β} to be the most parsimonious and we used it to further develop GPLake-S.

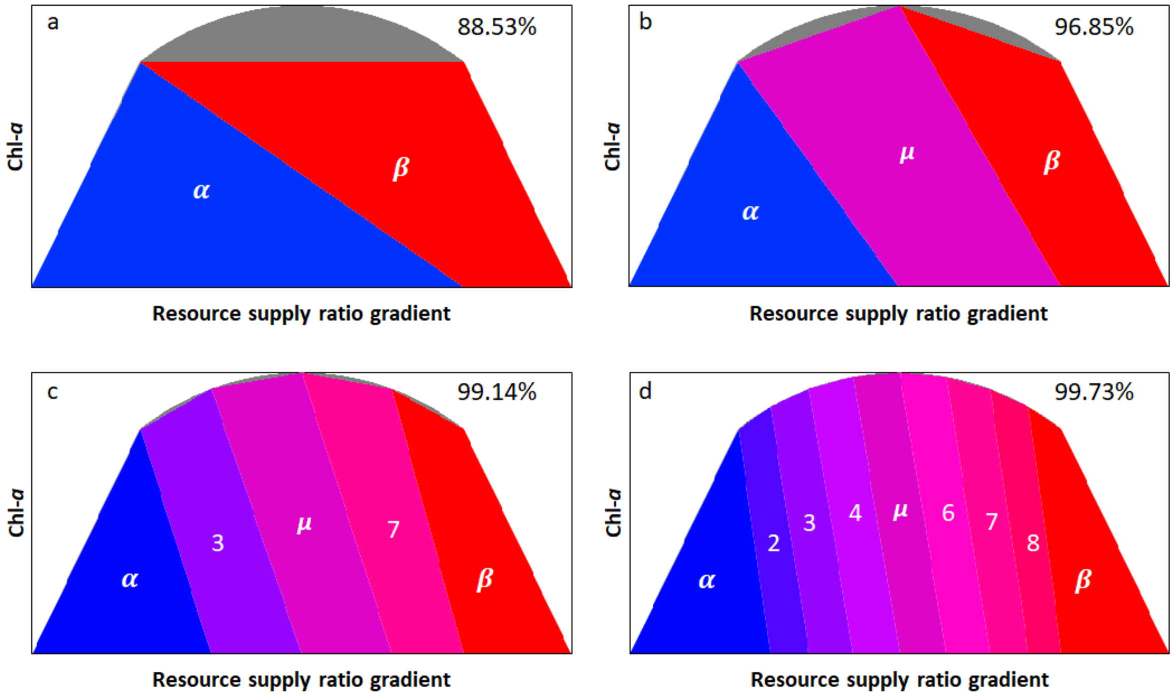

Figure 4.4 Theoretical analysis with the 2R2W (panel a), the 2R3W (panel b), the 2R5W (panel c) and the 2R9W TM models (panel d). In each panel the outcome of the 2RnW model with n going to infinity is shown as the concave curve in the zone of colimitation. The grey areas in each panel represent the difference between in chl-*a* between the latter model and each of the former models. In each panel, the percentage of the coloured area compared to the total (coloured + grey) area is given.

4.3.2 Derivation of GPLake-S

Having chosen to describe the community of phytoplankton in terms of three characteristic species W_α, W_μ and W_β we can now derive equations for the expected N^*, P^* and chl-a^* concentrations for any given combination of P_{in} and N_{in}. Here, α denotes the species with the highest N:P ratio while β represents species with the lowest N:P ratio and μ is the species that is intermediate in its requirements for P and N. For these three species we derived equations for the equilibrium chl-a^*, P^* and N^* concentration under five types of limitation: a P-limited system with a monoculture of W_α, a P and N colimited system with a coexistence of W_α and W_μ, a N and P colimited system with a coexistence of W_μ and W_β, a N-limited system with a monoculture of W_β, and finally a light limited system with an undefined coexistence of W_α, W_μ and W_β. These equations represent five planes with P_{in} as x-coordinate, N_{in} as the y-coordinate and chl-a as the zcoordinate of the plane. Please note that in deriving these equations we made the same assumption as in GPLake, namely that for realistic parameterizations of phytoplankton growing under nutrient limitation the R^* value of the limiting nutrient can be ignored because it hardly affects the equilibrium concentration W^*.

Plane 1) P-limited plane with monoculture of W_α:

$$Chl_P^* = \frac{D}{l}\frac{P_{in}}{c_{P,W_\alpha}} \tag{4.34}$$

$$N_P^* = N_{in} - \frac{c_{N,W_\alpha}}{c_{P,W_\alpha}}P_{in} \tag{4.35}$$

$$P_P^* = 0 \tag{4.36}$$

Plane 2) P- and N-limited plane with coexistence of species W_α and W_μ:

$$Chl_{PN}^* = \frac{D}{l}\frac{c_{P,W_\mu}N_{in} - c_{N,W_\mu}P_{in}}{c_{N,W_\alpha}c_{P,W_\mu} - c_{P,W_\alpha}c_{N,W_\mu}} + \frac{D}{l}\frac{c_{N,W_\alpha}P_{in} - c_{P,W_\alpha}N_{in}}{c_{N,W_\alpha}c_{P,W_\mu} - c_{P,W_\alpha}c_{N,W_\mu}} \tag{4.37}$$

$$N_{PN}^* = P_{PN}^* = 0 \tag{4.38}$$

Plane 3) N- and P-limited plane with coexistence of species W_μ and W_β:

$$Chl_{NP}^* = \frac{D}{l}\frac{c_{P,W_\beta}N_{in} - c_{N,W_\beta}P_{in}}{c_{N,W_\mu}c_{P,W_\beta} - c_{P,W_\mu}c_{N,W_\beta}} + \frac{D}{l}\frac{c_{N,W_\mu}P_{in} - c_{P,W_\mu}N_{in}}{c_{N,W_\mu}c_{P,W_\beta} - c_{P,W_\mu}c_{N,W_\beta}} \tag{4.39}$$

$$N_{NP}^* = P_{NP}^* = 0 \tag{4.40}$$

Plane 4) N-limited plane with monoculture of W_β:

$$Chl_N^* = \frac{D}{l}\frac{N_{in}}{c_{N,W_\beta}} \tag{4.41}$$

$$P_N^* = P_{in} - \frac{c_{P,W_\beta}}{c_{N,W_\beta}}N_{in} \tag{4.42}$$

$$N_N^* = 0 \tag{4.43}$$

Plane 5) Light-limited plane with undefined combination of species W_α, W_μ and/or W_β:

$$Chl_L^* = Plateau_{GPLake} \tag{4.44}$$

$$N_L^* = N_{in} - \frac{l}{D} c_{N,W_\mu} Plateau_{GPLake} \tag{4.45}$$

$$P_L^* = P_{in} - \frac{l}{D} c_{P,W_\mu} Plateau_{GPLake} \tag{4.46}$$

Please note that while GPLake-S does specify the relative abundance of the α, β and μ species in the light limited phase because we do not specify their characteristics with respect for competition for light we here assume that the stoichiometric composition of the phytoplankton under light limitation complies with that of the μ species.

Because each plane represents a limitation the realized equilibrium chl-a^* level is determined by

$$Chl_{GPLake-S}^* = min(Chl_P^*,\ Chl_{PN}^*,\ Chl_{NP}^*, Chl_N^*, Chl_L^*) \tag{4.47}$$

and the limiting factor can be identified. Once this limitation is known, the matching equations for calculating P^* and N^* can be applied. We call this model GPLake-S as it represents the stoichiometric extension of the original GPlake model. See Table 4.1 for a full list of symbols of GPLake-S with units and description.

Table 4.1 Unit and description of the symbols used in GPLake-S.

Symbol	Unit	Description
P_{in}	mg P m^{-3}	Inflowing phosphorus (P) concentration
N_{in}	mg N m^{-3}	Inflowing nitrogen (N) concentration
D	day^{-1}	Dilution rate (reciprocal of residence time)
l	day^{-1}	Phytoplankton community loss rate
$c_{P,W\alpha}$	g P g chl-a^{-1}	Stoichiometric constant of species α for P
$c_{N,W\alpha}$	g N g chl-a^{-1}	Stoichiometric constant of species α for N
$c_{P,W\mu}$	g P g chl-a^{-1}	Stoichiometric constant of species μ for P
$c_{N,W\mu}$	g N g chl-a^{-1}	Stoichiometric constant of species μ for N
$c_{P,W\beta}$	g P g chl-a^{-1}	Stoichiometric constant of species β for P
$c_{N,W\beta}$	g N g chl-a^{-1}	Stoichiometric constant of species β for N
Chl^*_P	mg chl-a m^{-3}	Chl-*a* level in the P-limited plane of GPLake-S
P^*_P	mg P m^{-3}	P concentration in the P-limited plane of GPLake-S
N^*_P	mg N m^{-3}	N concentration in the P-limited plane of GPLake-S
Chl^*_{PN}	mg chl-a m^{-3}	Chl-*a* level in the PN-colimitation plane of GPLake-S
P^*_{PN}	mg P m^{-3}	P concentration in the PN-colimitation plane of GPLake-S
N^*_{PN}	mg N m^{-3}	N concentration in the PN-colimitation plane of GPLake-S
Chl^*_{NP}	mg chl-a m^{-3}	Chl-*a* level in the NP-colimitation plane of GPLake-S
P^*_{NP}	mg P m^{-3}	P concentration in the NP-colimitation plane of GPLake-S
N^*_{NP}	mg N m^{-3}	N concentration in the NP-colimitation plane of GPLake-S
Chl^*_N	mg chl-a m^{-3}	Chl-*a* level in the N-limited plane of GPLake-S
P^*_N	mg P m^{-3}	P concentration in the N-limited plane of GPLake-S
N^*_N	mg N m^{-3}	N concentration in the N-limited plane of GPLake-S
Chl^*_L	mg chl m^{-3}	Chl-*a* level in the light limited plane of GPLake-S
P^*_L	mg P m^{-3}	P concentration in the light limited plane of GPLake-S
N^*_L	mg N m^{-3}	N concentration in the light limited plane of GPLake-S
$Slope_{GPLake}$	g chl-*a* g P^{-1}	GPLake parameter for chl-*a* level over inflowing resource concentration of P based on the characteristics of a lake
$Plateau_{GPLake}$	mg m^{-3}	GPLake parameter for chl-*a* level in the light limitation phase based on the characteristics of a lake

4.3.3 Parameterization of GPLake-S

To make actual calculations with GPLake-S we needed a set of parameters defining stoichiometric characteristics of the extreme species α and β and of the intermediate species μ in GPLake-S. Please note that we express N:P ratios throughout this study on a weight by weight basis. Empirically measured ranges of N:P mass ratios under field conditions are given by Downing et al., 1992. From their table we took the value of 20.0 for 'Algae, P-deficient' as an estimate of $c_{N,W\alpha}/c_{P,W\alpha}$ and their value of 7.0 for 'Algae, whole community' as an estimate of $c_{N,W\beta}/c_{P,W\beta}$. For empirically measured range of N:P ratios under experimental conditions we referred to the work by Klausmeier et al., 2004a and took their value of 20.0 for *Synechococcus spp.* as an estimate of $c_{N,W\alpha}/c_{N,W\alpha}$ and their value of 3.2 for *Melosira binderana* as an estimate of $c_{N,W\beta}/c_{P,W\beta}$. For model data we referred to the parameters of the BLOOM II model of phytoplankton dynamics (Los, 2009). Specifically, we used the values of 19.3 for *Aphanizomenon spp.* 'phosphorus type' as an estimate of $c_{N,W\alpha}/c_{P,W\alpha}$ and their value of 4.1 for *Microcystis spp.* 'nitrogen type' as an estimate of $c_{N,W\beta}/c_{P,W\beta}$. See Table 4.2 for an overview of these parameters. We assume that these data sources cover the stoichiometry variability of phytoplankton species in a wide range of P-deficient, N-deficient and colimitation conditions, and hence can provide a sufficiently wide range for the stoichiometric variability of a phytoplankton community under natural conditions. As explained above, we defined N:P mass ratio of the intermediate species W_μ through geometric averaging of the N:P mass ratios of the α and β species resulting in an estimate of $c_{N,W\mu}/c_{P,W\mu} = 9.44$.

Table 4.2 N:P mass ratios from sources of field, lab and model data. Values from literature in bold and geometrically averaged values in *italics*. All data sources see Appendix 4.3.

	N:P mass ratios			Reference
	$c_{N,W\alpha}/c_{P,W\alpha}$	$c_{N,W\mu}/c_{P,W\mu}$	$c_{N,W\beta}/c_{P,W\beta}$	
Field	**20.0**	*11.83*	**7.0**	Downing et al., 1992
Lab	**20.0**	*8.00*	**3.2**	Klausmeier et al., 2004a
Model	**19.3**	*8.90*	**4.1**	BLOOM II (Los, 2009)
Geometric average	*19.76*	*9.44*	*4.51*	

The next step in parameterizing GPLake-S consists of obtaining values of the stoichiometric constraints for the α, β and μ species. On basis of the BLOOM II parameter table (Rockström et al., 2009a) we choose $c_{P,W\mu}$ = 0.7 g P/g chl-*a* for the intermediate species. Setting this value allows us to calculate the other five stoichiometric constants. Given the average N:P mass ratio of 9.44 we get $c_{N,W\mu}$ = 6.61 g N/g chl-*a*. Next, we calculated the stoichiometric constants of the α and β species on basis of two considerations: 1) the ratio of N:P of the α and β species should comply with the estimate of $c_{N,W\alpha}/c_{P,W\alpha}$ *and* $c_{N,W\beta}/c_{P,W\beta}$, respectively and 2) the multiplication of the N and the P content of each species should obey a trade-off comparable to the tradeoff that we assume for the R^* values. Here this tradeoff is defined as $c_{P,W\alpha}\ c_{N,W\alpha} = c_{P,W\mu}\ c_{N,W\mu} = c_{P,W\beta}\ c_{N,W\beta}$. See Appendix 4.4 for the resulting equations and Table 4.3 for the resulting parameter values. The last step in the parameterization aims at making sure that GPLake-S complies with GPLake. We do so by making the assumption that GPLake represents the mono-culture of the μ species and that in GPLake the ratio of N_{in} and P_{in} complies with $c_{N,W\mu}/c_{P,W\mu}$. In that case we can make both model compatible by first calculating the *Slope* parameter of GPLake (Chang et al., 2019b) given the depth and residence time of the lake of interest and from there calculate the ratio between the dilution rate over the community loss rate of phytoplankton with the formula $[D/l] = c_{P,W\mu}\ Slope_{GPLake}$. Moreover, we can calculate the maximum level of chl-*a* at which light limitation sets in in GPLake-S on basis of the *Plateau* parameter of GPLake (Chang et al., 2019b) calculated for the same set of lake characteristics as was used for calculating the *Slope* parameter.

Table 4.3 Parameters and input of the default setting of GPLake-S for a lake with a depth of 2 meters and a residence time of 167 days. The *Slope* and *Plateau* parameter can be calculated with the tool provided as online material of Chang et al., 2019b. The ratio between the dilution rate and the loss rate of phytoplankton is calculated by $[D/l] = c_{P,W\mu}\ Slope_{GPLake}$.

Symbol	Value	Unit	Description
$c_{P,W\alpha}$	0.48	g P g chl-a^{-1}	Stoichiometric constant of species α for P
$c_{N,W\alpha}$	9.56	g N g chl-a^{-1}	Stoichiometric constant of species α for N
$c_{P,W\mu}$	0.70	g P g chl-a^{-1}	Stoichiometric constant of species μ for P
$c_{N,W\mu}$	6.61	g N g chl-a^{-1}	Stoichiometric constant of species μ for N
$c_{P,W\beta}$	1.01	g P g chl-a^{-1}	Stoichiometric constant of species β for P
$c_{N,W\beta}$	4.57	g N g chl-a^{-1}	Stoichiometric constant of species β for N
$Slope_{GPLake}$	0.689	g chl-a g P^{-1}	Response in chl-*a* concentration as a function of the inflowing resource concentration in case of nutrient limitation according to GPLake
$Plateau_{GPLake}$	97.0	mg chl-a m^{-3}	Maximum chl-*a* concentration due to light limitation according to GPLake
D/l	0.483	-	Dilution rate over the community loss rate of phytoplankton
P_{in}	variable	mg P m^{-3}	Inflowing P concentration
N_{in}	variable	mg N m^{-3}	Inflowing N concentration

4.3.4 Applying GPLake-S for combinations of inflowing nutrient concentrations

We are now in the position to make predictions of chl-*a* concentrations for any given combination of P_{in} and N_{in} based on the depth and residence time of the system of interest. In the example given here we focus on the same set of characteristics that was used as an example in GPLake (Chang et al., 2019b). This example deals with a lake a depth of 2 meters and a residence time of 167 days. The resulting values of the *Slope* and *Plateau* parameters of GPLake are 0.689 g chl-*a* g P^{-1} and 97.0 mg chl-*a* m^{-3}, respectively (Table 3b). Please note that these values of $Slope_{GPLake}$ and $Plateau_{GPLake}$ were obtained by calculating P_{in} in mg P m^{-3} from nutrient loading in mg P m^{-2} year^{-1} using Vollenweider method for normalization by water depth and residence time (see Equation 9 and the explanation thereof in Chang et al., 2019b). From there, the ratio between the dilution rate and the community loss rate of phytoplankton is calculated by $[D/l] = c_{P,W\mu}\ Slope_{GPLake}$. This resulted in a dimensionless value of 0.483 for *[D/l]*. With this we have values for all parameters needed to calculate the five planes of GPLake-S (each of them representing a specific type of limitation) according to the equations for $chl\text{-}a^*_{P}$, $chl\text{-}a^*_{PN}$, $chl\text{-}a^*_{NP}$, $chl\text{-}a^*_{N}$, *and* $chl\text{-}a^*_{L}$ as a function of P_{in} and N_{in} presented above. And as a final step, we calculated the predicted value of $chl\text{-}a^*_{GPLake\text{-}S}$ by taking the minimum of these values and in doing so identified which factor actually limits phytoplankton abundance. This knowledge then allowed us to calculate $P^*_{GPLake\text{-}S}$ and $N^*_{GPLake\text{-}S}$ by using the equations that match the limitation that occured. We present the outcomes of GPLake-S in this study for a range of inflowing P concentrations of $0 < P_{in} < 250$ mg P m^{-3} and on the basis of the average ratio between P and N in our modelled community of phytoplankton for a range of inflowing N concentrations of $0 < N_{in} < 2500$ mg N m^{-3}. The resulting values of $chl\text{-}a^*_{GPLake\text{-}S}$ are presented in Figure 4.5 by the intensity of the green color. This figure also shows which type of limitation occured for a given combination of P_{in} and N_{in}: P-limitation, PN-colimitation, NP-colimitation, N-limitation or light limitation. The equations for the lines that specify at which levels of inflowing nutrients switches between types of limitations for phytoplankton abundance in GPLake-S occur see Appendix 4.5.

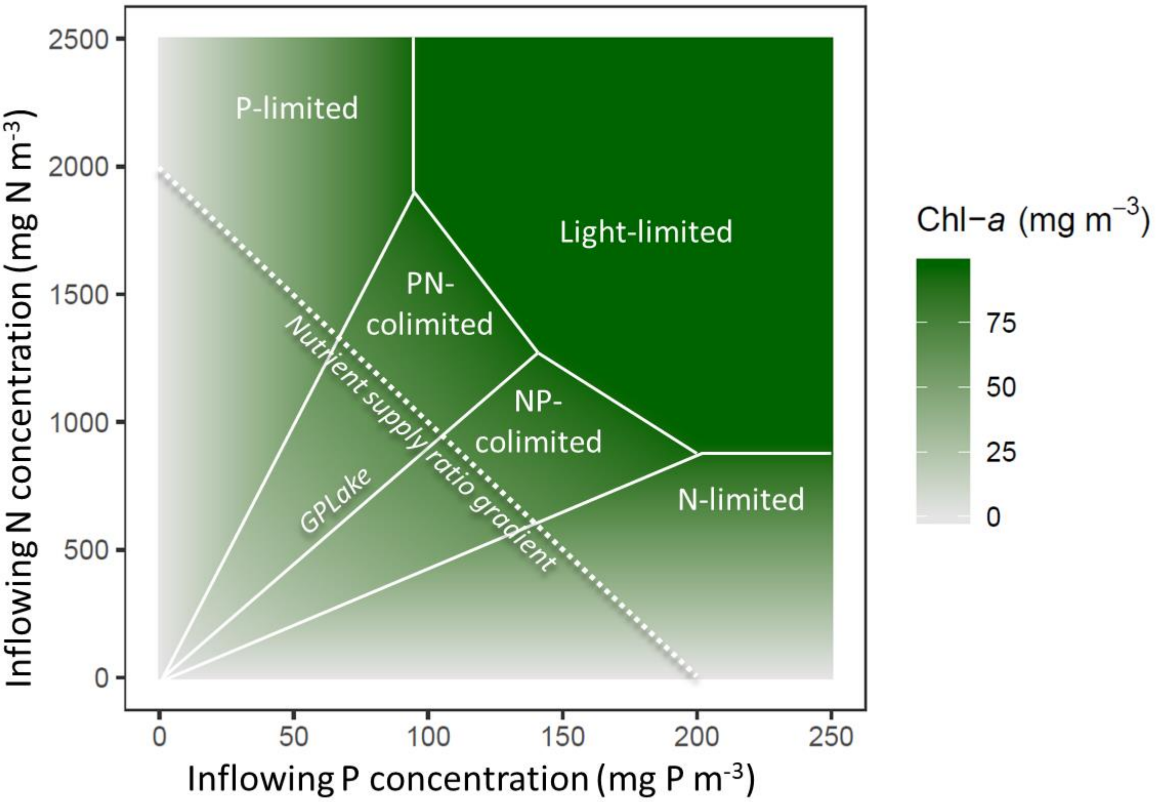

Figure 4.5 The predictions of chl-*a*$^{*}_{\mathrm{GPLake\text{-}S}}$ as a function of inflowing P_{in} and N_{in} concentrations. The figure clearly shows the P-limited plane, N-limited plane, the two colimitation planes and the light limited plane. The dotted line represents the nutrient supply ratio gradient that forms the x-axis of Figure 4.6. The line where the PN-colimitation meets the NP-colimitation corresponds to the prediction by GPLake (Chang et al., 2019b). Please refer to this study for details on how to calculate the inflowing nutrient concentration in mg m^{-3} from the nutrient loading in mg m^{-2} year^{-1} given the depth and residence time of the lake under study.

4.3.5 Applying GPLake-S along a nutrient supply ratio gradient

As a final step we compare our prediction of chl-*a* by GPLake-S along a nutrient supply ratio gradient (dashed line in Figure 4.5) against the predicted chl-*a* levels for each of the phytoplankton species and types that are covered by the BLOOM II model (Rockström et al., 2009a) and against the prediction made by GPLake (Chang et al., 2019b). To start with the latter comparison, GPLake focusses on P-limitation only while assuming that the supply of N varies accordingly to meet the stoichiometric demands of those phytoplankton species that are present in the system. This means that GPLake deals with those combinations of supply ratios that fall on the line that separates the PN-colimited from the NP-colimited planes of GPLake-S as depicted in Figure 4.5. And this also means that GPlake only makes predictions for a single point on the nutrient supply ratio gradient depicted in Figure 4.5. When compared with the predictions for phytoplankton species and types that are covered by the BLOOM II parameter table (see Appendix 4.3), two things catch the eye. Following the logic of our community expansion of the Tilman model for resource competition, each of these species is plotted along the nutrient supply ratio gradient according to its stoichiometric demands. The range in these demands closely matches the zones of PN and NP-colimitation. This stems from the fact that the range of stoichiometric demands of the species and types in BLOOM II coincides well with the combined range based on field, lab and model data presented in Table 4.2. With respect to chl-*a* predictions, the GPLake-S prediction matches the average of the wide variation in predictions per species and types from the BLOOM II parameter table (Figure 4.6).

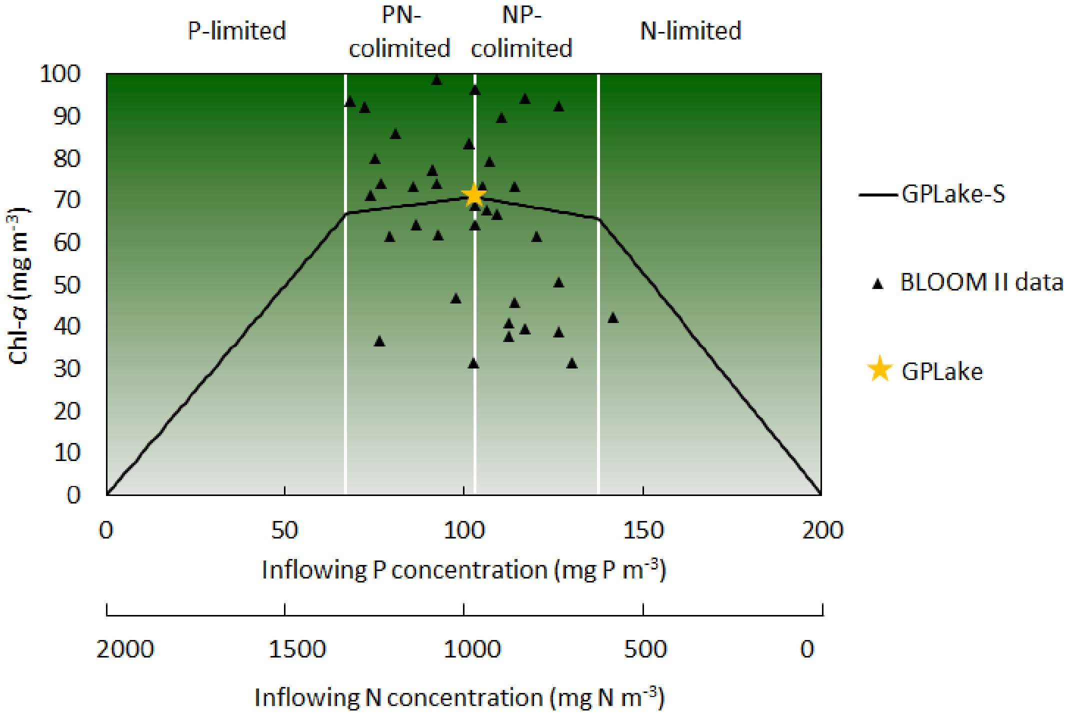

Figure 4.6 Comparison of the prediction of chl-*a* by GPLake-S (solid black line) along a nutrient supply ration gradient (dashed line in Figure 4.5) with the chl-*a* levels predicted for each of the phytoplankton species and types that is covered by the BLOOM II data (small triangles) and with the prediction made by GPLake (yellow star symbol).

4.4 Discussion

4.4.1 Towards a generically parameterized model of lake eutrophication that takes stoichiometric ratios and constraints into account

In developing GPLake-S we have taken an important step forward in understanding and predicting the impacts of eutrophication by multiple potentially limiting nutrients on phytoplankton abundance in natural systems. Our aims with the model are to provide water quality managers with a model that 1) is used for predicting chl-*a* concentrations considering combinations of P- and N-loadings; 2) can identify the limiting factor, i.e. phosphorus, nitrogen, both phosphorus and nitrogen, or light, of the target ecosystem; 3) can be parameterized with data sources from lab, field and model studies; 4) is easy to use and requires a limited number of inputs that are available to water quality managers. While eutrophication is often considered as a singular pressure, the body of evidence of it being two conjoint pressures in freshwater systems (namely P and N pollution) have become undeniable (Paerl et al., 2016b; Lewis et al., 2020). While ecological resource competition theory has long delved into such concepts, the link towards chl-*a* prediction using these models has remained largely absent. GPLake-S fills this gap, building on ecological resource competition theory to deliver a minimalist mechanistic model for predicting chl-*a* under scenarios of two competing nutrients. Our results of the GPLake-S model showed it to be capable of distinguishing between different types of limitation (N, P, N+P and light limitation) commonly described in real world lake systems (see e.g. Lewis et al., 2020), while predicting the resulting chl-*a* as a measure of phytoplankton abundance.

4.4.2 Design considerations underlying GPLake-S

The basis of the GPLake-S model is firmly rooted in ecological resource competition theory sensu Tillman and Huisman (Tilman, 1982; Huisman et al., 1995). The basis of stoichiometric limits (i.e. the α and β species) is well accepted in the field of ecological stoichiometry and has a clear empirical basis (Klausmeier et al., 2004b; Danger et al., 2008; Teurlincx et al., 2017). The selection of the optimal number of species to describe the nutrient to chl-*a* relationship (Figure 4.4) may be questioned, however. The concept of productivity and its link to biodiversity is often debated and examined in the context of Biodiversity-Ecosystem Functioning (BEF) literature (Striebel et al., 2009; Striebel et al., 2012; Jochum et al., 2020). Within the BEF framework, small increases in ecosystem functioning can often be attributed to increasing biodiversity, leading to the notion that the inclusion of more species in a model is per definition meaningful. Our goal, however, is somewhat different in that we are looking for first order estimations of phytoplankton abundance in the form of chl-*a* concentrations, not to answer the question regarding biodiversity and productivity per se. This has led us to choose what is model-wise the least complex solution with a reasonable fit. We argue that in the context of eutrophication management, biodiversity of the phytoplankton community is seldom the desired end goal. Rather, the questions posed in eutrophication management revolve around the amount of chl-*a* produced. Nonetheless, it is important to note that some level of biodiversity (i.e. three species) is necessary to make sound predictions of chl-*a*/nutrient relations, given our assumption of the characteristics of those species. Such interest for biodiversity in simple models has gained increasing traction in ecological consumer-resource based BEF modelling (Danger et al., 2008; Parain et al., 2018). Here we show that biodiversity is also important when using ecological consumer resource theory to predict chl-*a* as a measure of phytoplankton abundance.

4.4.3 The empirical basis of GPLake-S

There are in total eight parameters required to make apply GPLake-S: the six stoichiometric constants for P and N of the three species α, β and μ, the ratio between the dilution rate and the phytoplankton community loss rate and finally the maximum amount of chl-*a* due to light limitation. These latter two parameters are derived from the *Slope* and *Plateau* of GPLake. To calculate the *Slope* and *Plateau* of GPLake we need the c_1 and c_2 parameters of that model and the depth and residence time of the lake under consideration. The resulting parameters of GPLake-S for the default setting of GPLake for a lake with a depth of 2 meters and a residence time 167 days are given in Table 4.3 and the equations to calculate them in Appendix 4.4. Following the design principles of GPLake, we collected information about the stoichiometric variability in terms of maximum and minimum N:P ratios on the basis of field, lab and model data. N:P ratios of phytoplankton are widely published (Hillebrand et al., 2013; De Senerpont Domis et al., 2014; Tanioka et al., 2020) and have historically been used to define the limiting nutrient in lake ecosystems (see e.g. Faafeng et al., 1993). Less common is information about the P:chl-*a* and N:chl-*a* ratios needed to parameterize the six stoichiometric constants of GPLake-S. Of the three data sources used for the N:P ratios, only the BLOOM II parameter table also specifies the P:chl-*a* and N:chl-*a* ratios, using carbon content as an intermediate step. This is not a coincidence as the approach taken in the BLOOM II model overlaps with that of GPLake-S in the sense that both models recognize the importance of algal N:P ratios in predicting algal abundances and take into account that a semi-continuous range of those ratios is present in natural algal communities. For some of the basic design principles of BLOOM II, and how these relate to the Tilman model of ecological resource competition, see Appendix 4.6. Because this parameter is key to GPLake, we chose to estimate the stoichiometric constant of the intermediate species μ for phosphorus, $c_{P,W\mu}$, from the BLOOM II parameter table and calculated the other five stoichiometric constants on basis of that value using the equations provided in Appendix 4.4. One may question this approach for two reasons. What are the consequences of starting with the parametrization with $c_{P,W\mu}$ instead of one of the other five stoichiometric constants? And in what way are the predicted chl-*a* concentrations dependent on the specific value we chose, acknowledging that we used a single data source here in contradiction with the GPLake philosophy to combine the strength of field, lab and model data in finding generic parameters? The simple - but also surprising - answer to these questions is that neither the order of parametrization or even the value we chose for $c_{P,W\mu}$ has an impact on the chl-*a* concentrations predicted by GPLake-S. This is due to the fact that for reasons of compliance of GPLake-S with GPLake we estimate the ratio of the dilution rate over the phytoplankton community loss rate $[D/l]_{GPLake\text{-}S}$ by multiplying the *Slope* parameter obtained from GPLake by the estimated value of $c_{P,W\mu}$ according to the formula $[D/l] = c_{P,W\mu}\ Slope_{GPLake}$. Any change in our estimate of $c_{P,W\mu}$ will therefore result in a proportional change in $[D/l]_{GPLake\text{-}S}$. And in each of the equations of GPLake-S, be it the planes that predict the chl-*a* concentration as a function of P_{in} and N_{in} under the five different limitations, but also in the equations of the lines that specify the relation between P_{in} and N_{in} at which there is a switch in the type of limitation these proportional changes in each of the six stoichiometric constants and $[D/l]_{GPLake\text{-}S}$ will cancel out, leaving the predicted chl-*a* concentration and the type of limitation that occurs unchanged. This brings us to the important conclusion that GPLake-S inherits its estimates for the intermediate species that thrive under intermediate N:P ratios from the elaborate parametrization of GPLake on basis of the Vollenweider data, the selected lab experiments and the runs with PCLake. And also leads to the conclusion that the only additional empirical data to parameterize GPLake-S given a parameterized GPLake are the N:P ratios of the α and β species.

4.4.4 Omitting light-nutrient colimitation in GPLake

In the development of GPLake-S we expanded the contrast between nutrient and light limitation that is key to GPLake to the concept of nutrient colimitation. In combination with the choice to represent stoichiometric variability in natural communities of phytoplankton in three species α, β and μ that represent a high, low and intermediate N:P ratio this results in five possible types of limitation as depicted in Figure 4.5. Of course, these limitations are only a subset of the factors that might limit phytoplankton abundance under natural conditions. Prominent among these factors is the colimitation of light and nutrients (Brauer et al., 2012). This occurs when in the light gradient (over depth) phytoplankton is nutrient limited near the surface but light limited near the sediment. While addressing such colimitation would fit in our philosophy of GPLake-S with respect to ecological complexity we omitted it for the practical reason that we do not know of analytical expressions for the equilibrium values of chl-*a* under such colimitation. Adding light-nutrient limitation would therefore prohibit us from developing a simple tool for applying GPLake-S in water quality management, e.g. cause technical complexity to the use of GPLake-S that we considered undesirable. As a result, the predictions of GPLake-S for P_{in} and N_{in} values for which light-nutrient colimitation would likely occur will be overestimates because they ignore a type of limitation that we know operates in the field. Being necessarily an overestimate, the GPLake-S chl-*a* should therefore be seen as a worst case scenario under those circumstances (Figure 4.7).

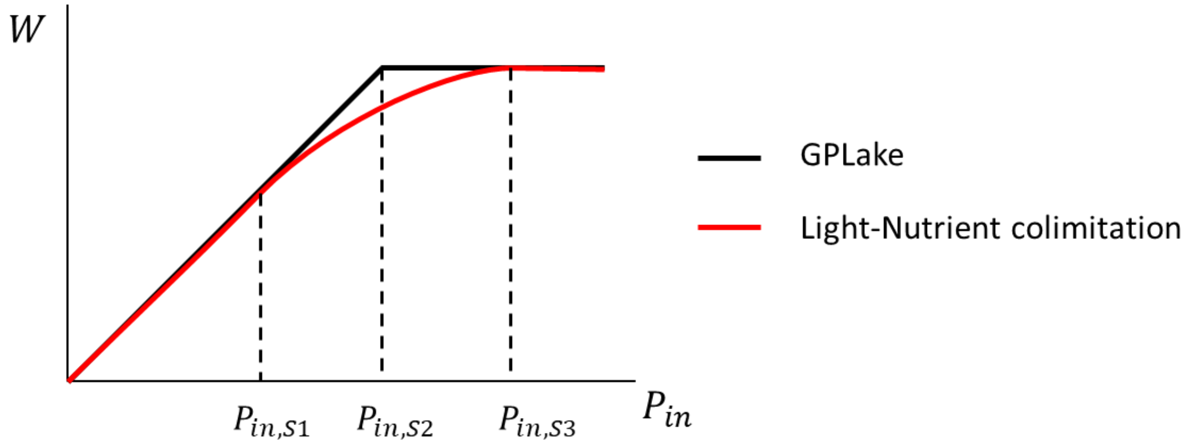

Figure 4.7 The impact of taking light-nutrient colimitation into account for the gradient studied in GPLake. In GPLake algal abundance is either nutrient or light limited depending on whether the actual value of P_{in} is lower or higher than a critical level $P_{in,S2}$, respectively. When light-nutrient colimitation is taken into account, two critical levels of P_{in} arise. Below critical level $P_{in,S1}$ the whole column is nutrient limited and above a critical value $P_{in,S3}$ the whole column is light limited. If the actual value of P_{in} is between $P_{in,S1}$ and $P_{in,S3}$ the upper layer of the column is nutrient limited and the lower layer of the column is light limited. This conceptual graph clearly shows that adding this new type of limitation necessarily lowers the predicted phytoplankton abundance and the simplification made in GPLake and GPLake-S should therefore be seen as a worst case scenario with respect to the phenomenon of light-nutrient colimitation.

4.4.5 Relevance for water management and policy

Freshwater eutrophication management and policy has a long history of focusing on the reduction of phosphorus inputs to lakes to attempt to revert the damage to the ecosystem by anthropogenic pollution (see e.g. Carpenter et al., 1999). Whether lakes respond and can be recovered by P-loading alone is an ongoing and long lasting scientific discussion (see e.g. Schindler et al., 2016 and Paerl et al., 2016b). Increasing evidence of colimitation of lake systems across large spatial scales (Lewis et al., 2020) is suggesting that both nutrients can be limiting to phytoplankton abundance, and therefore can be relevant to consider when diagnosing lake eutrophication issues. GPLake-S allows a first order estimate of chl-*a* while allowing for colimitation (as well as single nutrient limitation), offering a simple, mechanistic tool to managers to determine the state of their lake given the nutrient loading (see Appendix 4.7 for a simple Excel GPLake-S tool). Reducing nutrient loads, either N or P, may be achieved through a variety of management interventions and measures, but is strongly dependent on the shape of the response of chl-*a* to nutrient loading (Schallenberg, 2020). This response to a reduction in P-loading may be markedly different than response of the lake system to a reduction of N-loading, making the consideration of both nutrients in management assessment relevant. GPLake-S offers a simple, yet mechanistic and theory based model that can be used to make a first-order assessment of the chl-*a* levels and the impacts of both P and N reduction efficacy, all with limited data requirements. Only by considering both nutrients and their impact on the lake phytoplankton chl-*a* levels can water managers make cost effective decisions with maximal ecological recovery. Ecological recovery from anthropogenic restoration is needed to meet the growing demands of both nature, biodiversity and humanity on these freshwater ecosystems (Mueller et al., 2016; Janssen et al., 2020).

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Chapter 5

Exploring how cyanobacterial traits affect nutrient loading thresholds in shallow lakes: a modelling approach

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Abstract

Globally, many shallow lakes have shifted from a clear macrophyte-dominated state to a turbid phytoplankton-dominated state due to eutrophication. Such shifts are often accompanied by toxic cyanobacterial blooms, with specialized traits including buoyancy regulation and nitrogen fixation. Previous work has focused on how these traits contribute to cyanobacterial competitiveness. Yet, little is known on how these traits affect the value of nutrient loading thresholds of shallow lakes. These thresholds are defined as the nutrient loading at which lakes shift water quality state. Here, we used a modelling approach to estimate the effects of traits on nutrient loading thresholds. We incorporated cyanobacterial traits in the process-based ecosystem model PCLake+, known for its ability to determine nutrient loading thresholds. Four scenarios were simulated, including cyanobacteria without traits, with buoyancy regulation, with nitrogen fixation, and with both traits. Nutrient loading thresholds were obtained under N-limited, P-limited, and colimited conditions. Results show that cyanobacterial traits can impede lake restoration actions aimed at removing cyanobacterial blooms via nutrient loading reduction. However, these traits hardly affect the nutrient loading thresholds for clear lakes experiencing eutrophication. Our results provide references for nutrient loading thresholds and draw attention to cyanobacterial traits during the remediation of eutrophic water bodies.

5.1 Introduction

Globally, many shallow lakes have shifted from a clear macrophyte-dominated state to a turbid phytoplankton-dominated state due to eutrophication (Hallegraeff, 1993; Anderson et al., 2002; Heisler et al., 2008). Such a shift in water quality state is often accompanied by toxic cyanobacterial blooms and their subsequent nuisance properties (Paerl, 1988; Huisman et al., 2018). Driven by wind, these blooms can float to shoreline areas, threatening drinking water safety and deteriorating recreational values of lakes (Chorus et al., 2000; Qin et al., 2010; Wurtsbaugh et al., 2019). Therefore, lake managers aim to restore their lakes to a clear state that can usually provide more societally relevant ecosystem functions compared to a turbid state (Bachmann et al., 1999; Hilt et al., 2017; Janssen et al., 2020). However, restoration of these lakes is often challenging because of the lack of response of lakes to measures such as reducing nutrients (Jeppesen et al., 2007c).

This lack of response of shallow lakes originates from the positive feedback between macrophytes and phytoplankton, resulting in resistance to external pressures such as changing nutrient loading (Scheffer et al., 1993; Scheffer et al., 2001; Suding et al., 2004). Due to this resistance, a clear or turbid state of a lake can remain itself until a threshold of nutrient loading, hereafter referred to as nutrient loading threshold, is crossed. This nutrient loading threshold is also known as the critical nutrient loading (van Liere et al., 2007; Janse et al., 2008; Janse et al., 2010; Xu et al., 2015; Janssen et al., 2017). In shallow lake ecosystems, there are usually two values of nutrient loading thresholds. One value is identified during the process of eutrophication when a lake shifts from clear to turbid. This value can assist managers and decision-makers with setting limits on nutrient loading to prevent a lake shifting to a turbid state with a typically inevitable loss of ecosystem services (Janssen et al., 2020). The other value is identified during the process of oligotrophication when a lake shifts from a turbid to a clear state. This value can be used to set the target of nutrient loading reduction in lake restoration actions aiming at improving the water quality of a eutrophic lake (Janssen et al., 2017). Cyanobacteria as the dominant species in eutrophic shallow lakes have the potential to challenge water quality improvement (Scheffer et al., 1997). They have benefited from a long evolutionary history during which traits have developed and provided them with competitive advantages such as buoyancy regulation and nitrogen fixation (Paerl et al., 2009). These traits promote access to light and nutrients accessibility for cyanobacteria and can have impacts on lake nutrient loading thresholds.

Buoyancy regulation is a trait that allows cyanobacteria to rapidly adjust their vertical position in the water column (Ibelings et al., 1991; Huisman et al., 2004). The advantage of buoyancy regulation for cyanobacteria is well recognized, as it supports cyanobacterial biomass by providing access to light at the surface and outcompetes the other phytoplankton species through shading (Dokulil et al., 2000; Paerl et al., 2013; Huisman et al., 2018). Buoyancy regulation is achieved in two ways that involve cell- and colony-level processes. At the cellular level, buoyancy regulation is provided by gas vesicles in cells of some cyanobacterial species, e.g., *Microcystis*, *Dolichospermum* (formerly *Anabaena*), and Oscillatoria (Walsby, 1994). These gas vesicles allow cyanobacteria cells to have a lower density than water so that they can float (Walsby, 1994). At a colonial level, buoyancy regulation is enhanced by a colony formation that enlarges the colony radius, thereby increasing the buoyancy (Reynolds et al., 1987). These colonies with high buoyancy can persist at the surface for lengthy periods and enable cyanobacteria to become dominant, especially in warm, eutrophic and stagnant water bodies (Paerl, 2009; Ma et al., 2016).

Nitrogen fixation allows cyanobacteria to utilize atmospheric nitrogen as a source of nitrogen. Therefore, nitrogen-fixing cyanobacteria have an advantage over non-nitrogen fixers when nitrogen is deficient (Agawin et al., 2007), which occurs when nitrogen loading is relatively low or when the denitrification rate is high in the water column (Paerl, 1990; Dokulil et al., 2000; Ferber et al., 2004). Nitrogen fixation is an energy-consuming process that requires cyanobacteria to utilize sufficient light (Bothe et al., 2010; Paerl et al., 2013). The aforementioned buoyancy regulation trait provides cyanobacteria ample access to light, which may then facilitate energy-intensive nitrogen fixation. Examples of cyanobacterial genera known for nitrogen fixation are Dolichospermum and Aphanizomenon (Fogg, 1971; Paerl et al., 2000).

Previous work has mainly focused on how these traits contribute to cyanobacterial competitive strength (Reynolds et al., 1987; Vitousek et al., 2002; Huisman et al., 2004; Huisman et al., 2018), yet there is little known about how these traits affect the value of nutrient loading thresholds of shallow lakes. The values of nutrient loading threshold are typically obtained using a modelling approach (Janssen et al., 2017), since studies on critical transitions based on field data are rare due to the requirements of long time series (Baron et al., 2011; Capon et al., 2015; Gsell et al., 2016; Hilt et al., 2018) and mesocosm experiments cannot represent the field situation (Barker et al., 2008; Stewart et al., 2013; Chang et al., 2019b). Moreover, models can analyse the nutrient loading threshold for almost unlimited scenarios without disturbing the lake. Cottingham et al., 2015 used a simple mathematical model to show that cyanobacterial traits can reduce lake resistance to external nutrient loading and accelerate eutrophication. Yet, their approach lacks real ecosystem processes such as food web interactions and competition between phytoplankton and macrophytes, thus making a useful evaluation of the effect of cyanobacterial traits on nutrient loading thresholds difficult. For this purpose, a process-based model that incorporates biogeochemical processes is needed as a good tool to study the effect of cyanobacterial traits on the value of nutrient loading threshold (van Liere et al., 2007; Janse et al., 2008; Janssen et al., 2017).

In this study, we incorporated established knowledge from empirical research on buoyancy regulation and nitrogen fixation into a process-based ecosystem model. Then, to account for different combinations of cyanobacterial traits, we analysed four conceptual scenarios where cyanobacteria have no traits, one of the two traits, or both traits, respectively. Because different N:P loading ratios lead to different nutrient limitations (Elser et al., 2009), each scenario was simulated with a low (nitrogen-limited), a high (phosphorus-limited) and an intermediate (colimited) N:P weight ratios. Through this modelling effort, we evaluated how the cyanobacterial traits of buoyancy regulation and nitrogen fixation affect nutrient loading thresholds during lake eutrophication and oligotrophication.

5.2 Methods

5.2.1 Model Selection

We used a modelling approach to explore the effect of cyanobacterial traits on nutrient loading thresholds at the ecosystem level. We chose to use PCLake+ (Janssen et al., 2019b), which is the updated version of PCLake (Janse, 2005), as the model is known for its ability to calculate nutrient loading thresholds. PCLake+ was deemed suitable for our study for four reasons. First, PCLake+ can represent real lake ecosystems because it incorporates complex biogeochemical processes, including nutrient cycling, phytoplankton species and macrophyte competition, and zooplankton and fish food web interactions. Second, processes and interactions of cyanobacteria developed in this model have been validated (Janse, 2005; Mellios et al., 2015; Janssen et al., 2017). Third, PCLake+ can be used in bifurcation analyses to identify nutrient loading thresholds during lake eutrophication and oligotrophication (Janse, 2005; Mooij et al., 2007; Janse et al., 2008; Janssen et al., 2017). Finally, DATM (Database Approach To Modelling) provides an interface where the framework of equations used in PCLake+ is explicitly presented. This explicit framework enabled us to easily incorporate new processes by changing or adding equations to the model (Mooij et al., 2014; Van Gerven et al., 2015).

5.2.2 Model Adaptation

Using established knowledge from empirical research, we expanded PCLake+ by adding and modifying equations for the cyanobacterial traits buoyancy regulation and nitrogen fixation.

5.2.2.1 Buoyancy Regulation

To incorporate buoyancy regulation in PCLake+, we coded an additional surface layer on the top of the existing epilimnion layer. Moreover, we developed a new state variable for cyanobacteria that are present in the newly developed surface layer (hereafter referred to as “surface cyanobacteria”). The equations for growth and mortality processes of the surface cyanobacteria were coded similarly to the original equations of cyanobacteria in the epilimnion. The equation for light intensity in the water column was adjusted to account for extinction caused by surface cyanobacteria. As a result, surface cyanobacterial blooms can shade macrophytes and phytoplankton species such as chlorophytes and diatoms while competing for nutrients in the water column. In addition, we included an equation that accounts for reduced oxygen aeration rate when dense surface cyanobacteria hinder the interactions between water and atmosphere (Ploug, 2008). This process was included in a similar method as the equation applied for the floating plant *Lemna* in PCDitch (Janse, 1998; van Liere et al., 2007).

Empirical research shows that buoyancy regulation by cyanobacteria depends on wind, temperature, and biomass conditions (Ibelings et al., 2003; Qin et al., 2016). Strong winds disable the formation of floating layers. Studies have shown that wind speed above a certain threshold causes turbulence that can disperse cyanobacterial colonies, thereby impeding buoyancy (Wu et al., 2009; Wu et al., 2013). Temperature provides energy for cyanobacteria to produce the protein-forming gas vesicles (Thomas et al., 1986). These gas vesicles can lower the cyanobacterial cell density below water density, enabling cyanobacteria to float (Thomas et al., 1986; Pfeifer, 2012). Conversely, cyanobacterial cells start settling when the temperature is too low to support gas vesicle production, such as during autumnal sedimentation (Visser et al., 1995). High levels of cyanobacterial biomass can indirectly facilitate buoyancy regulation because of colony formation (Dokulil et al., 2000; Kong et al., 2005). Cyanobacterial colonies have higher buoyancy compared to individual cells (Visser et al., 1997), enabling cyanobacterial colonies to remain at the surface for a longer period during summer compared to noncolony-forming species (Wu et al., 2009; Medrano et al., 2016).

For these three processes, we defined the actual floating speed F_f (m d^{-1}) of the planktonic cyanobacteria in PCLake+ by using a maximum floating speed F_{max} (m d^{-1}) times three limitation factors for wind speed (σ_W), temperature (σ_T), and biomass (σ_B), as shown in Equation (5.1).

$$F_f = F_{max}\,\sigma_W\,\sigma_T\,\sigma_B \tag{5.1}$$

Each limiting factor was defined as a Hill equation, following a similar concept of a step function as used in the book by Alon, 2019 (Equations (5.2–4)),

$$\sigma_W = 1 - \frac{W^b}{H_W^b + W^b} \tag{5.2}$$

$$\sigma_T = \frac{T^b}{H_T^b + T^b} \tag{5.3}$$

$$\sigma_B = \frac{B^b}{H_B^b + B^b} \tag{5.4}$$

in which W, T, and B are wind speed, temperature, and biomass, respectively; σ_W, σ_T, and σ_B are limitation factors for floating caused by wind, temperature, and biomass, respectively; transition constants H_W, H_T, and H_B were defined to mark the transition between limited and unlimited conditions for wind speed, temperature, and biomass, respectively; and b is the coefficient that defines the smoothness of the Hill equation. Values of Equations (5.2–4) vary between zero and one where a value of zero denotes serious limitation and one denotes no limitation. For example, the wind limitation factor (Equation (5.2)) will approach zero if the wind speed W exceeds the transition constant H_W. Similarly, buoyancy regulation becomes limited if the temperature and biomass are below their transition constants (note the sign of b).

Following empirical research (see for references Table 5.1), we set the transition constants for wind at 3 m s^{-1}, for temperature as 15 °C, and for biomass at 10 mg chl-*a* m^{-3} (Table 5.1). We selected 10 m day^{-1} as the maximum floating speed (Table 5.1). Both biomass and temperature are dynamically calculated in the model. We applied a constant wind speed of 2 m s^{-1}, which is lower than the transition constant so that the wind will not hinder buoyancy regulation in this study. Net floating speed F_{net} (m day^{-1}) was defined by an actual floating speed F_f (m day^{-1}) minus the settling speed S (m day^{-1}) that depends on resuspension and temperature (Equation (5.5)).

$$F_{net} = F_f - S \tag{5.5}$$

Table 5.1 Applied transition constants and maximum floating speed for the calculation of actual floating speed of cyanobacteria in PCLake+.

Parameter	Description	Reference Value	Applied Value	Unit	Model Notation
H_W	Transition constant of wind speed	3–4[a, b, c, d], 2[e, f], 2–3[g], 4[h]	3	m s^{-1}	cVWindThrBlue
H_T	Transition constant of temperature	12–18[i, j]	15	°C	cTmThrBlue
H_B	Transition constant of cyanobacterial biomass (expressed as chl-*a* level)	10–100[a], 100[k], 20[l]	10	mg chl-*a* m^{-3}	cChlaThrBlue
W_{max}	Maximum floating speed	1–10[k], 4.5[m], 6[n], 0.2–250[o], 10[p]	10	m d^{-1}	cVFloMaxBlueW

[a] Qin et al., 2016; [b] Cao et al., 2006 ; [c] Webster et al., 1994; [d] O'Brien et al., 2004; [e] Huang et al., 2012; [f] Wallace et al., 2000; [g] Wu et al., 2009; [h] Reynolds et al., 1987; [i] Visser et al., 1995; [j] Carey et al., 2012; [k] Sherman et al., 1994; [l] Xu et al., 2015; [m] Reynolds et al., 1975; [n] Kromkamp et al., 1990; [o] Bormans et al., 1999; [p] Wang et al., 2012.

5.2.2.2 Nitrogen Fixation

Besides available NH_4^+ and NO_3^- in the water column, nitrogen fixation generates additional nitrogen loading from the atmosphere that is neglected in the original PCLake+ model. Here, we developed equations to account for these extra sources of nitrogen in terms of dissolved N_2 to planktonic and benthic cyanobacteria. Therefore, cyanobacteria with nitrogen fixation in the expanded PCLake+ can use the nitrogen pools of NH_4^+, NO_3^-, and dissolved N_2.

Many empirical studies have shown that nitrogen fixation requires substantial energy and hence is dependent on light intensity (Fogg, 1971; Paerl et al., 1979; Severin et al., 2008). For this positive relationship between light intensity and nitrogen fixation rates, we used the model from Ferber et al., 2004, which expanded upon the model by Levine et al., 1987, as shown in Equations (5.6) and (5.7):

$$N_i = N_S - N_S e^{-a} + D \tag{5.6}$$

$$a = \alpha N_S^{-1} I_{ave} \tag{5.7}$$

in which N_i (µgN mgChl^{-1} day^{-1}) is the fixation of nitrogen at certain light intensity I_{ave} (J m^{-2} s^{-1}), N_S (µgN mgChl^{-1} day^{-1}) is fixation at light saturation, D (µgN mgChl^{-1} day^{-1}) is fixation in the dark, and α is the slope of the rising limb of the relationship between fixation and light intensity. The parameter units used in Ferber et al., 2004 were converted to the parameter units used in PCLake+. To simplify the calculation of a (Equation (5.7)), we combined αN_S^{-1} ((J m^{-2} s^{-1})$^{-1}$) as one constant parameter. Original and applied values of parameters are provided in Table 5.2. In addition, the light intensity I_{ave} was calculated by averaging the integral of light intensity through depth according to the Beer–Lambert law:

$$I_{ave} = \frac{I_{in} - I_{in} e^{-kZ}}{kZ} \tag{5.8}$$

in which I_{in} (J m^{-2} s^{-1}) is the light intensity at the surface, k (m^{-1}) is the total light extinction in the water column, and Z (m) is the lake depth.

Table 5.2 Parameter values adopted in PCLake+ used for the nitrogen fixation process. The parameter units used in Ferber et al., 2004 were converted to be the parameter units that can be coupled with current processes in PCLake+.

Parameter	Description	Reference Value *	Applied Value	Model Notation
N_S	Nitrogen fixation rate at light saturation	366 nmol N_2 (10^6 heterocysts)$^{-1}$ h^{-1}	60 μgN mgChl^{-1} day^{-1}	cNfixMaxBlue
D	Nitrogen fixation rate in the dark	58 nmol N_2 (10^6 heterocysts)$^{-1}$ h^{-1}	9.5 μgN mgChl^{-1} day^{-1}	cNfixDarkBlue
αN_S^{-1}	Auxiliary parameter for nitrogen fixation–light curve	2.16 (Ei m^{-2})$^{-1}$	0.036 (J m^{-2} s^{-1})$^{-1}$	cAlphNfix
I_{ave}	The average of integral light through depth	dynamically calculated (Ei m^{-2})	dynamically calculated (J m^{-2} s^{-1})	aLPARAveSurf, aLPARAveEpi, aLPARAveHyp

*** For the conversion method from reference value to applied value see Appendix 5.1.**

5.2.3 Bifurcation Analyses

To study the effect of buoyancy regulation and nitrogen fixation on the nutrient loading thresholds, we used the bifurcation analyses (Kiseleva et al., 2010; Janssen et al., 2017) with the expanded version of PCLake+. A bifurcation analysis is a mathematical tool to study large sudden changes in the output (here chl-*a*) as a result of small changes in the input (here nutrient load). A large sudden change indicates a nutrient loading threshold. Using bifurcation analyses to identify nutrient loading thresholds require several steps. Firstly, a range of nutrient loadings along a wide gradient needs to be defined. Secondly, the model needs to be run to equilibrium for each of these nutrient loadings in the selected range to calculate the chl-*a* at equilibrium. Thirdly, a curve can be drawn showing the response of chl-*a* levels to nutrient loading using the results of the equilibrium chl-*a* level as the y-axis and the corresponding nutrient loading as the x-axis. With this type of curve, a bifurcation plot can be obtained. Finally, the nutrient loading thresholds can be thus defined as the point of a sudden change in chl-*a* level in the bifurcation plot.

A bifurcation plot for shallow lakes commonly shows two lines (for example, see Janse et al., 2008; Janse et al., 2010); one line shows the results of simulations starting with a highly oligotrophic macrophyte-dominated state and commonly has a high nutrient loading threshold. The other line shows the results of simulations starting from a highly eutrophic phytoplankton-dominated state and commonly has a low nutrient loading threshold. The initial states needed to calculate these two lines can be set by using the values of state variables that represent an excessively clear and an excessively turbid state, respectively. These values are calibrated by Janse, 2005. The line with a high nutrient loading threshold can show a sudden increase of the chl-*a* level during eutrophication and illustrate the process of a lake shifting from a clear to a turbid state. The line with a low nutrient loading threshold can show a sudden decrease of chl-*a* level during oligotrophication and illustrate the process of a lake shifting from a turbid to a clear state.

In our study, each bifurcation analysis consists of 400 simulations for which 200 are used to calculate the oligotrophication line and 200 to calculate the eutrophication line. Both lines are calculated using a range of N-loads with 200 equal intervals between 0.0005 and 0.046 gN m^{-2} day^{-1}. We verified that the sudden changes in chl-*a* level are visible within this range of nutrient loadings. Each simulation was run for 50 years to reach the equilibrium. We then calculated the yearly average of the fiftieth year. From the 200 values for yearly averaged chl-*a*, we constructed one line of the bifurcation plot.

We performed the bifurcation analyses for scenarios with different combinations of the traits buoyancy regulation and nitrogen fixation. The four scenarios that we used are (1) a control scenario with neither buoyancy regulation nor nitrogen fixation (CT), (2) a scenario with only buoyancy regulation (BR), (3) a scenario with only nitrogen fixation (NF), and (4) a scenario where the cyanobacteria could both regulate buoyancy and fix nitrogen (BR + NF). We expect that the effects of cyanobacterial traits on the nutrient loading thresholds depend at least in part on the N:P ratio of the incoming load, which in return can lead to different nutrient limitations. We chose to set the N:P ratio at 5 for nitrogen-limitation, 20 for phosphorus-limitation, and 10 for colimitation. We applied the different N:P ratios by dividing the N-loads by 5, 10, or 20, respectively, to set the P-loads. In total, we performed 12 bifurcation analyses to assess all combinations of the four scenarios with the three N:P ratios.

We used the nutrient loading thresholds of the control scenario without traits as a benchmark and calculated its differences with the other three scenarios with traits under different N:P ratios. Besides the typical bifurcation plots that provide the nutrient loading threshold, we also reported phytoplankton composition to interpret the role of cyanobacterial traits in their competition with other algal species for different nutrient loadings. Because there are in total 12 scenarios and each of them requires 400 simulations to obtain a bifurcation plot, an R script was used to automatically activate the expanded PCLake+ under the DATM framework and perform these simulations (the script is shown in Appendix 5.2).

All model analyses performed in this study used a lake depth of 2 m and assumed complete vertical mixing. We note that PCLake+ is provided with an epilimnion and hypolimnion layer that can stratify (Janssen et al., 2019b). We did not use these functionalities for this study because a sudden shift in the water quality state of deep lakes is less common (Scheffer et al., 2001). Nevertheless, we implemented the traits for both layers to cater to future studies of deep lakes. All equations, as well as state and parameter values, are presented in Appendix 5.3. The full model can be downloaded from https://github.com/pcmodel/PCModel/tree/master/Licence_agreement/I_accept/PCModel1350/PCModel/3.00/Models/PCLake+/6.13.16/DATM/Chang_et_al_2020_Water.

5.3 Results

Bifurcation analyses with the expanded version of PCLake+ showed that cyanobacterial traits affected nutrient loading thresholds (Figure 5.1). Compared with the control scenario, the results for scenarios with traits show reduced nutrient loading thresholds for the shift from turbid to clear (Figure 5.2). The reductions in the nutrient loading threshold vary between 12% and 46%

(compared to a control where cyanobacteria lack these traits) depending on the limiting nutrient and the different cyanobacterial traits. The NF scenario showed the most reduction in the nutrient loading threshold when the N:P ratio was 5 (Figure 5.2). The BR+NF scenario showed the most reduction when the N:P ratio was 10. When the N:P ratio was 20, the NF scenario showed no effect on the nutrient loading threshold and the BR and BR + NF gave a comparable reduction in the nutrient loading thresholds during oligotrophication. Additionally, the chl-*a* levels of all scenarios with cyanobacterial traits revealed a different biomass in the turbid state compared to the CT scenario, except for the NF scenario under an N:P ratio of 20, where the two overlapped. Detailed results for each scenario are described in the sections below. The nutrient loading thresholds for the shift from clear to turbid were similar between all the scenarios (Figure 5.2). This suggests that once the cyanobacteria are dominant, the traits enable cyanobacteria to withstand efforts to eliminate them through nutrient reduction, whereas their emergence during eutrophication is hardly affected.

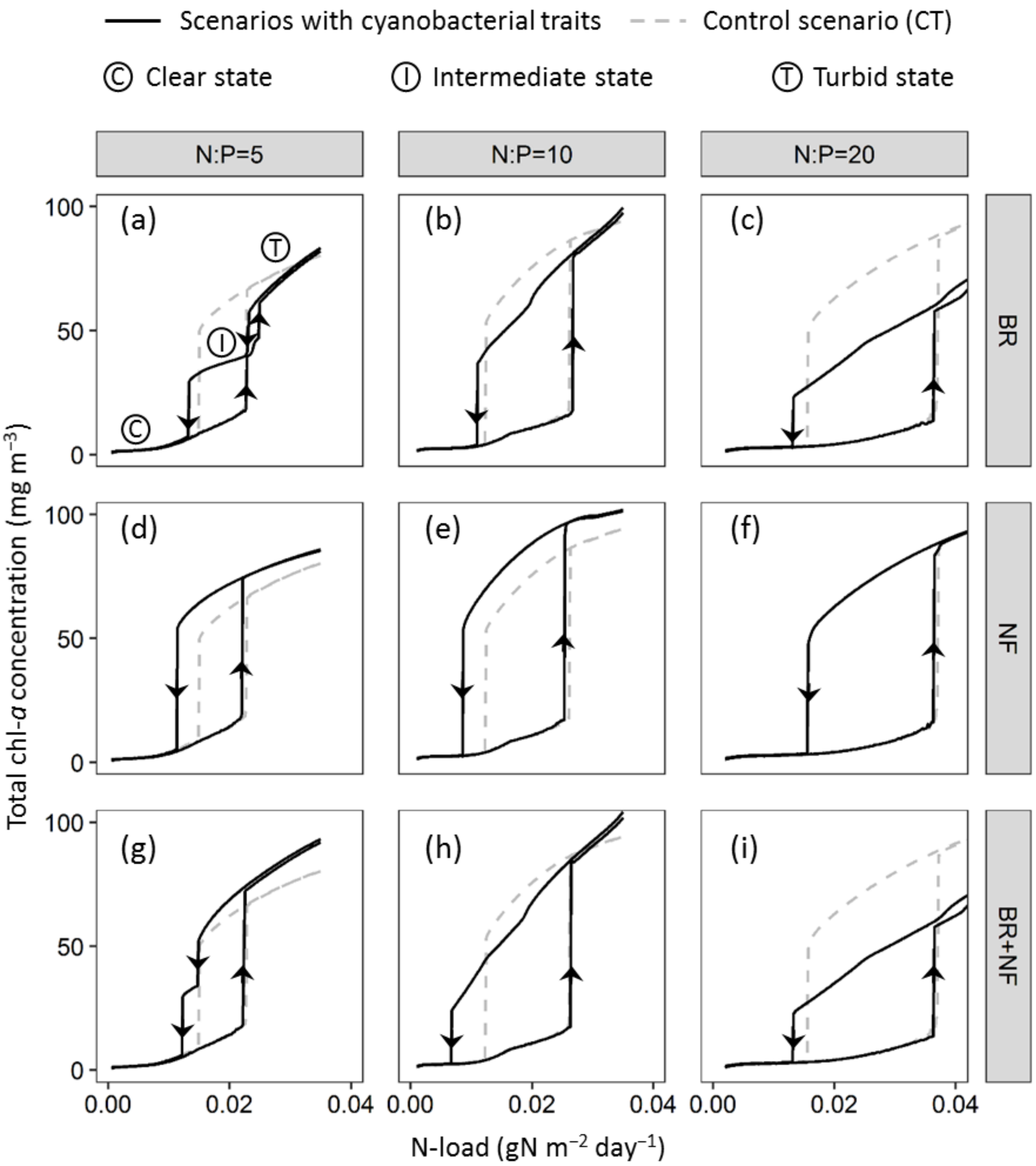


Figure 5.1 Bifurcation plots of total chl-*a* concentration for different scenarios of cyanobacterial traits (black lines) compared to the control (grey dashed lines: default PCLake+). The scenarios shown in the figure are (a–c) buoyancy regulation (BR), (d–f) nitrogen fixation (NF), and (g–i) combination of buoyancy regulation and nitrogen fixation (BR + NF). Simulations started from a turbid initial state are marked by arrows downwards, simulations started from a clear initial state are marked by arrows upwards.

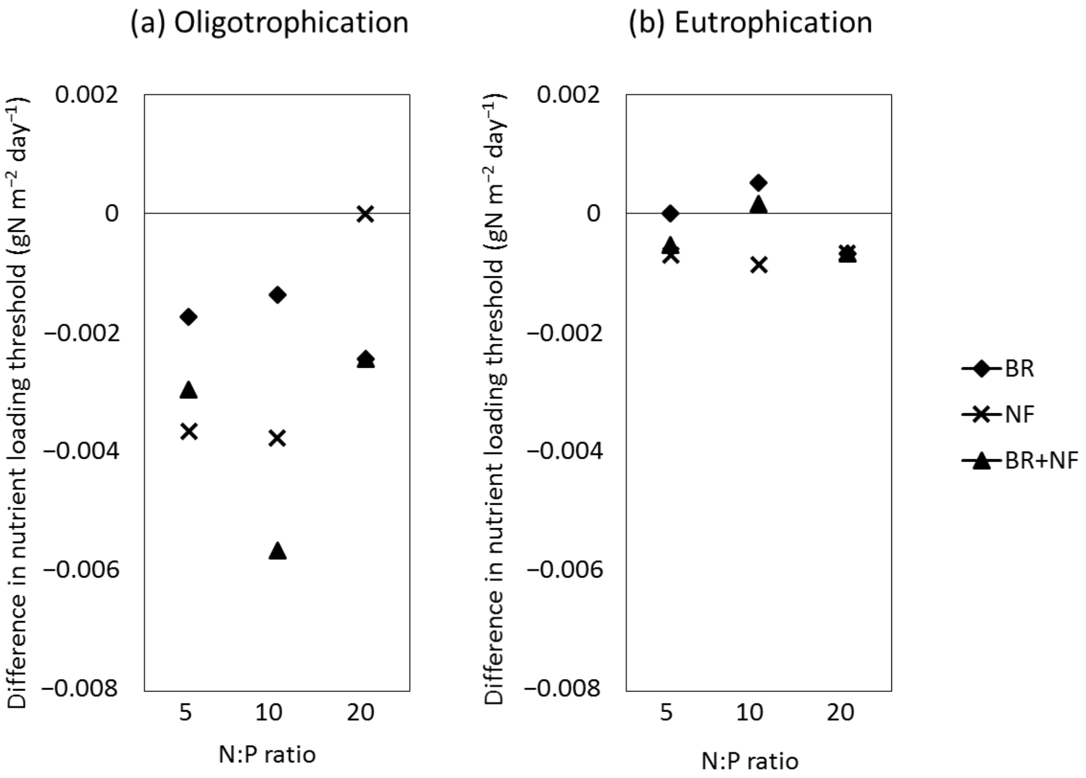


Figure 5.2 Differences in nutrient loading threshold between the control (CT) scenario and scenarios with traits, including the buoyancy regulation (BR) scenario with diamonds, the nitrogen fixation (NF) scenario with crosses, and the combination of buoyancy regulation and nitrogen fixation (BR + NF) scenario with triangles. (a) The difference of nutrient loading threshold obtained during oligotrophication and (b) the difference of nutrient loading threshold obtained during eutrophication.

5.3.1 Effect of Buoyancy Regulation (BR Scenario)

Inclusion of buoyancy regulation in the model led to a reduction of the chl-*a* levels from 9% to 40% just after the lake shifted from a clear to turbid state (Figure 5.1a–c). Yet, with increasing nutrient loadings, the chl-*a* levels show a stronger increase in the BR scenario compared with the CT scenario. Consequently, the chl-*a* level of the BR scenario surpassed the chl-*a* level of the CT scenario in the high nutrient loading scenario (see N:P is 5 and 10 in the graph, N:P is 20 and off-graph). For the BR scenario with different N:P ratios, the shape of the bifurcation plots showed three states. The first two are the clear macrophyte-dominated state where chl-*a* level is low and a turbid phytoplankton-dominated state where chl-*a* level is high. These two states are typically seen in shallow lakes (Scheffer et al., 1993). The third is an intermediate state where phytoplankton outcompete macrophytes (Figure A5.1) and chl-*a* level is intermediately high (“I“ in Figure 5.1a). While the eutrophication line follows the typical pattern of a bifurcation plot of shallow lakes, the oligotrophication line with an N:P ratio of 5 started with a turbid state (“T“ in Figure 5.1a) and shifted to an intermediate state (“I“ in Figure 5.1a) before returning to a clear state (“C“ in Figure 5.1a). Figure 5.3 demonstrates cyanobacterial dominance in the turbid state while diatoms are dominant in both the intermediate and clear states. Further, surface cyanobacteria were present when the scenario accounted for buoyancy regulation and they had higher biomass than the cyanobacteria in the water column, except during the intermediate state.

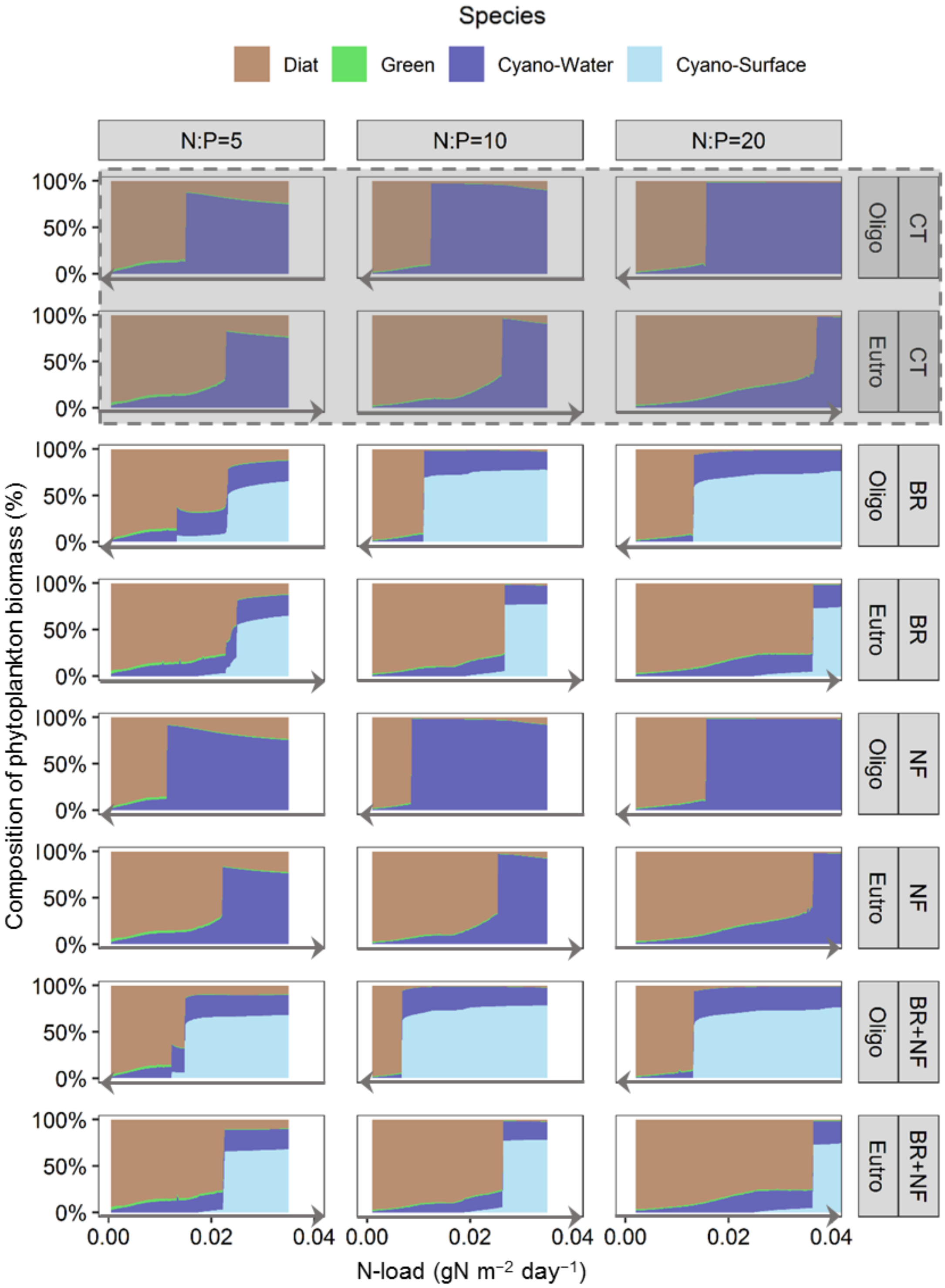


Figure 5.3 Composition of phytoplankton biomass in different scenarios during oligotrophication (Oligo) and eutrophication (Eutro) from bifurcation analyses. The grey box with dashed lines presents the results of the control (CT) scenario. Other scenarios shown in the figure are, from top to bottom, buoyancy regulation (BR), nitrogen fixation (NF), and a combination of buoyancy regulation and nitrogen fixation (BR + NF). Simulations started from a turbid initial state are marked by arrows towards the left; simulations started from a clear initial state are marked by arrows towards the right.

5.3.2 Effect of Nitrogen Fixation (NF Scenario)

As shown in Figure 5.1d–f, the addition of nitrogen fixation to the model increased the chl-*a* level when nitrogen was limited for phytoplankton, i.e., with an N:P ratio of 5 and 10. The chl-*a* level of the NF scenario overlapped with the CT scenario when the N:P ratio was 20 because sufficient nitrogen was available. The phytoplankton composition of the NF scenario was similar to the CT scenario with an exception around the position of nutrient loading thresholds. In both NF and CT scenarios, buoyancy regulation was disabled in the model simulations and the surface cyanobacteria were absent. Cyanobacteria in the water column were dominant when the lake was in a turbid state and diatoms were dominant within the phytoplankton community when the lake was in a clear state (Figure 5.3).

5.3.3 Synergistic Effect of Buoyancy Regulation and Nitrogen Fixation (BR + NF Scenario)

For the BR + NF scenario, the model showed a strong reduction of the nutrient loading thresholds during oligotrophication (Figure 5.1g–i). The triangles in Figure 5.2 showed that the combined effect of buoyancy regulation and nitrogen fixation on the nutrient loading thresholds was largest when the N:P ratio was 10, compared with all the other N:P ratios. As shown in Figure 5.2a, the difference between the nutrient loading thresholds of the CT scenario and the BR + NF scenario during oligotrophication was less than that of the NF scenario when the N:P ratio was 5, and identical to the BR scenario when the N:P ratio was 20. Like the BR scenario, the BR + NF scenario showed an intermediate state when the N:P ratio was 5 (Figure 5.1g). The intermediate state in the BR + NF scenario is shorter compared with the BR scenario. However, similar to the BR scenario when chl-*a* was at an intermediate level, macrophytes were absent (Figure A5.1) and diatoms were dominant (Figure 5.3). The chl-*a* level of the BR + NF scenario was higher than the chl-*a* level in the CT scenario when the N:P ratio was 5, but lower than the chl-*a* level in the CT scenario when the N:P ratio was either 10 or 20. Similarly to the BR scenario, in a turbid state, the chl-*a* level of the BR + NF scenario showed a more rapid increase than the chl-*a* level in the CT scenario as the nutrient loading increased. This led the chl-*a* level in the BR + NF scenario to surpass the chl-*a* level in the CT scenario when high nutrient loadings were applied in the simulations. Figure 5.3 shows that, under the BR + NF scenario, surface cyanobacteria were dominant when the lake was in a turbid state. This phytoplankton composition was comparable to the BR scenario.

5.4 Discussion

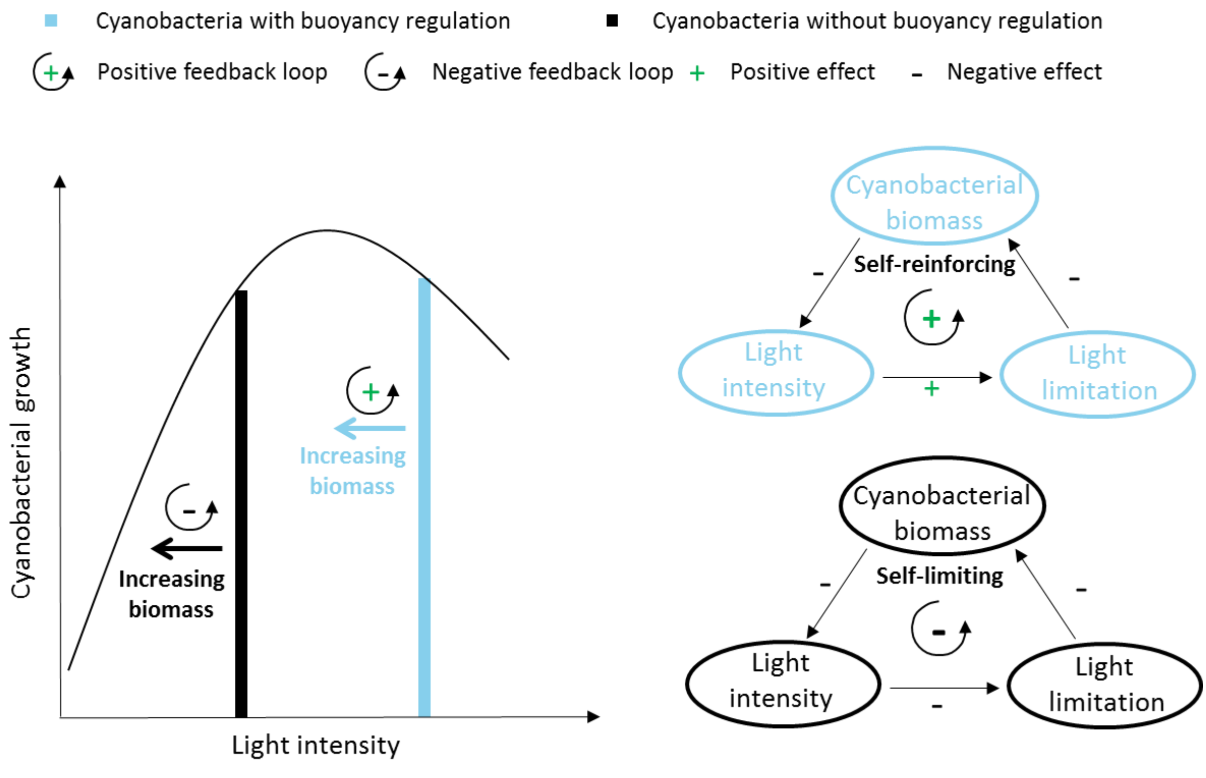
Our results obtained through bifurcation analyses with the expanded PCLake+ model indicate that the cyanobacterial traits of buoyancy regulation and nitrogen fixation reduce the value of nutrient loading thresholds, especially during oligotrophication. These effects on the nutrient loading thresholds differ between combinations of traits as captured in the four scenarios and with the limiting nutrients as expressed by the three N:P ratios. These results suggest that cyanobacterial traits can impede the effect of reducing nutrient loadings that are aiming to restore turbid lakes to their clear states. In contrast, small differences in nutrient loading thresholds between the control scenario and scenarios with traits suggest that cyanobacterial traits have a small effect on the shift in state during eutrophication.

5.4.1 Effect on Nutrient Loading Threshold

A reduction in nutrient loading threshold suggests an increase in the resistance of the turbid phytoplankton-dominated state to efforts of nutrient loading reduction. The underlying mechanisms of increasing resistance can be described with different feedback loops affected by cyanobacterial traits.

5.4.1.1 Feedback Loops Due to Buoyancy Regulation

The inclusion of buoyancy regulation results in a positive self-reinforcing feedback loop illustrated in Figure 5.4. In this positive feedback loop, the increase of cyanobacterial biomass results in lower light intensity but facilitates cyanobacterial growth even more. The effect of photoinhibition on surface cyanobacteria makes them less limited by light at high biomass and more limited by light at low biomass (Figure A5.2 in Appendix 5.4). As a result, cyanobacteria capable of buoyancy regulation are more resistant to nutrient reduction measures compared to cyanobacteria that do not have this trait. In comparison, cyanobacteria without buoyancy regulation (Figure 5.2, black line) usually experience a lower light intensity at which the increasing biomass will have a negative impact on itself, as shown by the negative feedback loop in Figure 5.4b.



(a) (b)

Figure 5.4 The relation between cyanobacterial growth and light intensity and the resulting feedback loop that self-reinforces or self-limits cyanobacterial biomass. (a) The cyanobacterial photosynthesis-irradiance (PI) curve showing the effect of light on cyanobacterial growth. The light blue bar is positioned at higher light intensity than the black bar because the cyanobacteria with buoyancy regulation can float to the surface and achieve a higher light intensity than the cyanobacteria staying in the water column. (b) The feedback loops of cyanobacterial biomass in response to light for the situation with (blue) and without buoyancy regulation (black).

5.4.1.2 Feedback Loops Due to Nitrogen Fixation

Nitrogen fixation provides biologically available nitrogen to cyanobacteria, allowing them to achieve high levels of biomass0(Tsygankov, 2007). In turn, higher cyanobacterial biomass increases the amount of nitrogen that can be fixed from dissolved N_2. As a result, nitrogen fixation leads to a positive feedback loop (Figure 5.5) from which cyanobacteria can benefit by becoming less nitrogen-limited compared to non-nitrogen fixers (Figure A5.3 in Appendix 5.4). Consequently, cyanobacteria that fix nitrogen are more resistant to nutrient-reduction measures compared to cyanobacteria that do not have this trait. This feedback loop provides most resistance in the nitrogen-limited system and is absent in the nitrogen sufficient system.

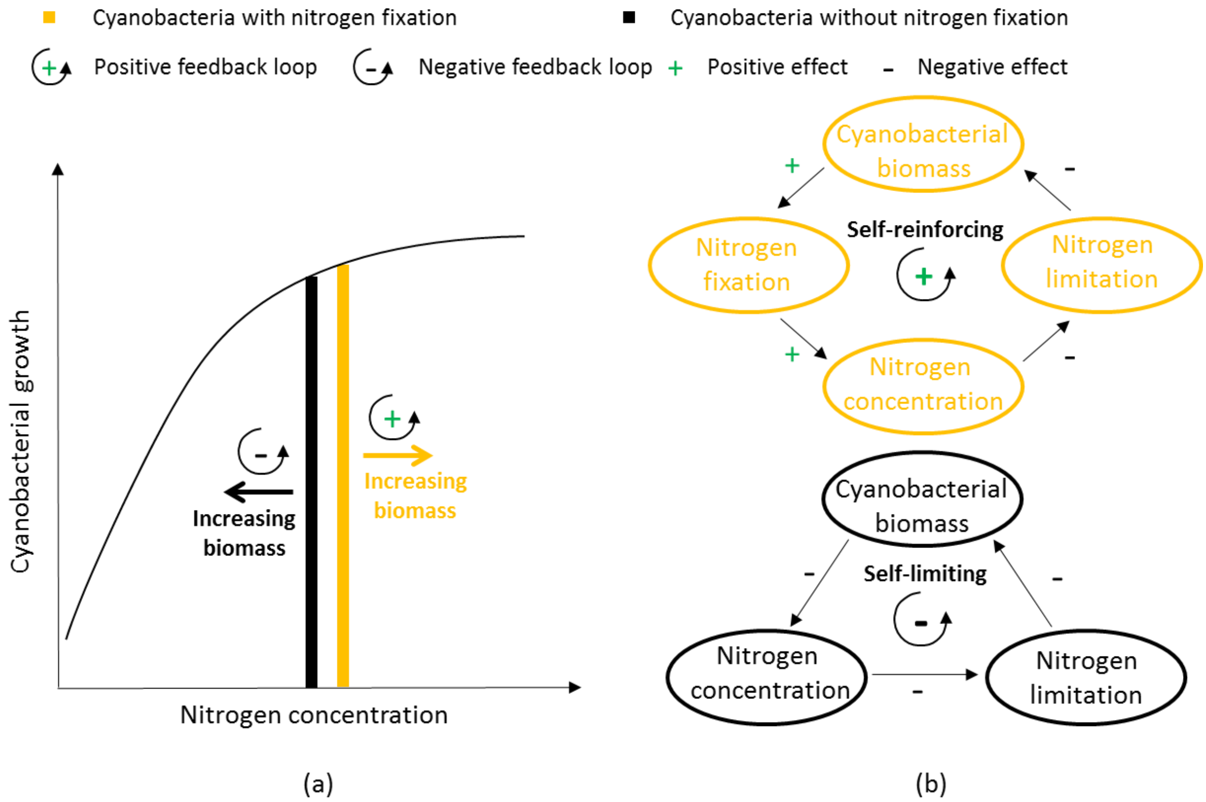


Figure 5.5 The relation between cyanobacterial growth and nitrogen concentration along with the resulting feedback loop that self-reinforces or self-limits cyanobacterial biomass. (a) The curve shows a positive relationship between nitrogen concentration and cyanobacterial growth. The yellow bar and the black bar are in a similar position since both types of cyanobacteria contain similar nitrogen concentrations in the water column. (b) The feedback loop of cyanobacteria with (yellow) and without nitrogen fixation (black).

5.4.1.3 Feedback Loops Due to the Combination of the Two Traits

The impact of the combined cyanobacterial traits on nutrient loading threshold depends on the interplay of the two positive feedback loops of buoyancy regulation and nitrogen fixation (Figure 5.6). Buoyancy regulation enables more light availability for cyanobacteria so that the nitrogen fixation rate is maximized, thereby enhancing the nitrogen fixation feedback loop, as shown at the right in Figure 5.6. The increased nitrogen availability from nitrogen fixation supports growth of cyanobacteria and helps cyanobacteria approach the biomass needed to reduce photoinhibition, hence strengthening the feedback loop of the buoyancy regulation, as shown at the left in Figure 5.6. Consequently, cyanobacteria that have both traits are more resistant to nutrient-reduction measures compared to cyanobacteria that do not have any traits. Moreover, in real-world situations, cyanobacteria are known to exhibit a suite of other traits that make them more resistant to high light intensities at the surface (see e.g., Paerl et al., 1983; Paerl et al., 1985). Besides these two positive feedback loops, which are individually caused by buoyancy regulation and nitrogen fixation, the interplay between these two traits generate a third, negative, feedback loop (middle of Figure 5.6). This negative feedback loop causes biomass of cyanobacteria to decrease the light availability and lead to a reduction of nitrogen fixation rate, limiting the cyanobacterial biomass. This negative feedback loop is especially relevant in cases where a relatively small part of the cyanobacterial biomass is present at the surface layer; this small proportion of surface cyanobacteria still shades the cyanobacteria in the water column, leading to sub-optimal nitrogen fixation. We found that this negative feedback loop was present when the N:P ratio was 5. In this condition, cyanobacteria rely on extra N from nitrogen fixation to compensate for the nitrogen limitation but are unable to because of the lower light intensity (Figure A5.4). This interpretation is consistent with our results shown in Figure 5.2a that when N:P was 5, the single nitrogen fixation (NF scenario) has a larger effect on nutrient loading thresholds than the combination of two traits (BR + NF scenario).

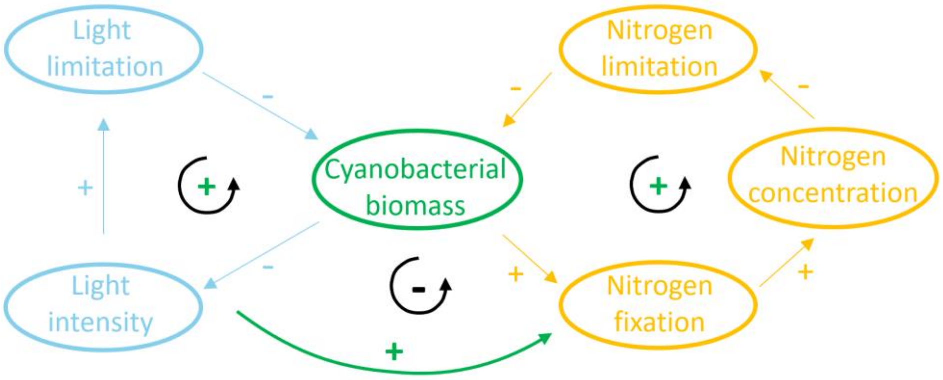


Figure 5.6 Feedback loop showing the combination of buoyancy regulation and nitrogen fixation. The relevant mechanisms of buoyancy regulation and nitrogen fixation are noted in blue and yellow, respectively. The interplay of the two functions is denoted in thick green arrows. The circular arrows denote positive or negative feedback loops, shown by a green plus sign and a black minus sign, respectively.

5.4.1.4 Effect on Lake Nutrient Loading Thresholds during Eutrophication

While these cyanobacterial traits reduced the nutrient loading thresholds during oligotrophication, they had little effect on determining the nutrient loading threshold during eutrophication. These nearly unaffected nutrient loading thresholds can be explained by the near absence of cyanobacteria in the clear macrophyte-dominated state. This can be explained from the positive feedback loops (Figures 4–6) that play a negligible role in the clear state. Also, the resistance of macrophytes to prevent a clear lake to become turbid due to eutrophication remains nearly unchanged. In contrast, the previous finding by Cottingham et al., 2015 shows that cyanobacterial traits can reduce the resistance of a clear ecosystem to eutrophication. The model used by Cottingham et al., 2015 is a simple conceptual model that lacks the effect of macrophytes and other food web components, whereas we simulated the nutrient loading thresholds with a process-based ecosystem model. The difference in model structures may explain the divergent conclusions of whether cyanobacterial traits can influence the resistance of a clear ecosystem to eutrophication.

5.4.2 Comparison to Natural Conditions

In contrast to our modelling study, most cyanobacterial blooms are a mixture of different types of cyanobacteria species that can fix nitrogen (e.g., *Nostoc* Paerl, 1990), regulate buoyancy (e.g., *Microcystis* and *Oscillatoria* Walsby, 1994), or do both (e.g., *Dolichospermum* and *Aphanizomenon* Li et al., 2016; Huisman et al., 2018). Their composition can be dynamic due to intraspecies competition under varying environmental conditions, such as light, temperature, and nutrients Shan et al., 2019. Here, we aimed to specify the effect of each cyanobacterial trait on determining the value of the nutrient loading thresholds. Our scenarios should, therefore, be seen as representative of functional groups in a case where one of the types of cyanobacterial species becomes dominant in the field. Simulations for intraspecies competition of cyanobacteria are outside the scope of this study.

Cyanobacteria with only buoyancy regulation usually outcompete cyanobacteria that have both nitrogen fixation and buoyancy traits (e.g., *Dolichospermum*) because they grow better under low light and use combined nitrogen more efficiently (Paerl et al., 2014). Moreover, nitrogen fixation is an energy-demanding process (Tsygankov, 2007). As a result of high energy costs, nitrogen-fixing cyanobacteria in a relatively N-rich environment have no competitive advantage, as shown in laboratory and field studies (Levine et al., 1999; Huisman et al., 2005). In a highly nitrogen-limited situation, however, nitrogen fixation can be advantageous to cyanobacteria. This is in line with our model results where we found that cyanobacteria with nitrogen fixation only affected the value of nutrient loading threshold in a nitrogen-limited or colimited environment (Figure 5.2). However, shallow lakes commonly appear to be phosphorus limited or colimited (Abell et al., 2012; Bratt et al., 2019). Our scenarios for phosphorus limited lakes show that cyanobacteria with buoyancy as traits have the highest effect on the nutrient loading threshold during oligotrophication. Under colimitation, our results indicate that cyanobacteria with both traits have the largest impact on the nutrient loading threshold during oligotrophication (Figure 5.2).

Despite the capacity of cyanobacteria with buoyancy regulation to reduce the value of the nutrient loading thresholds during oligotrophication, our results also showed that their biomass during this transition is lower compared to cyanobacteria that do not have buoyancy regulation. Instead, these surface cyanobacteria obtained the highest biomass under hypereutrophic conditions where light is limiting (Figure 5.1). This can be explained by the photoinhibition caused by high light intensity on the surface that can only be reduced when surface blooms reach high biomass (Tilzer, 1987; Ibelings et al., 1998; Gerla et al., 2011). In reality, the photoinhibition caused by high light intensity may not be observed due to cyanobacterial adaptation (Paerl et al., 1985) or high turbidity that lower the light intensity in the water column (Chaffin et al., 2012). Besides, there is no spatial heterogeneity present in the surface layer in terms of cyanobacterial biomass (i.e., it is assumed to be a homogenous layer that is continually mixed). This results in all of the cyanobacteria in the surface layer negatively impacted by high light intensity due to photoinhibition. In the field, buoyant cyanobacteria are distributed heterogeneously along with depth, hence the cyanobacteria on the topmost surface can shelter other cyanobacteria from the high light intensity and eliminate photoinhibition (Lichtenberg et al., 2020). Considering these findings, photoinhibition simulated in this study leads to a conservative prediction of cyanobacteria biomass compared with *in situ* conditions.

5.4.3 Modelling as a Tool for Lake Managers

The decrease in the value of nutrient loading thresholds due to the cyanobacterial traits, buoyancy regulation and nitrogen fixation, hinders attempts to improve water quality. Models such as PCLake+ can assist lake managers by calculating the nutrient loading threshold for lakes worldwide (Waajen et al., 2016; Janssen et al., 2017; Hilt et al., 2018; Li et al., 2019). The tool we have developed here—an extension to the PCLake+ model—allows both scientists and managers to analyse a wide range of scenarios related to buoyancy regulation and nitrogen fixation, and allows for calculations of relevant nutrient loading limits at the local and catchment scale (Teurlincx et al., 2019). Besides, the result of our study can be applied in the remediation of eutrophic lakes because it shows at what N:P ratio the shallow lakes become either oligotrophic or eutrophic. Moreover, tools like PCLake+ can be used to study the effect of these traits on nutrient loading thresholds among a large variety of lakes by applying different lake characteristics (e.g., area and sediment type). Finally, the expanded PCLake+ model can be coupled with a hydrodynamic model to study cyanobacterial bloom dynamics in networks of water bodies or to predict the cyanobacteria scum in a spatially heterogeneous system (see e.g., Taihu in Janssen et al., 2017). Overall, this model enables scientists and managers to understand the underlying mechanism of lake resistance and to predict required nutrient reduction as the remedy to lakes suffering from cyanobacteria, thereby moving towards a sustainable future in the Anthropocene (Downing et al., 2020).

5.5 Conclusions

To mitigate cyanobacterial blooms, it is important to estimate the effects of cyanobacterial traits on the effort that is needed to reduce nutrient loadings. Here we used a modelling approach and found that nutrient loading thresholds of shallow lakes were lowered due to cyanobacterial buoyancy regulation and nitrogen fixation, especially during oligotrophication. Moreover, we explained the changes in nutrient loading thresholds by clarifying the positive feedback loops that involve buoyancy regulation and nitrogen fixation. These results help explain how these traits enhance the resistance of a lake’s turbid, phytoplankton-dominated state to nutrient-reducing measures intended to achieve a clear macrophyte-dominated state. Our results point to the need to consider phytoplankton traits in lake management because they can hinder the effectiveness of measures to improve the water quality.

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Chapter 6

Discussion

6.1 Using consumer-resource interactions to derive nutrient thresholds

Consumer-resource interaction theory forms the backbone of this thesis, being applied to derive nutrient thresholds from very broad to very specific perspectives. First, models based on the consumer-resource interactions between human beings and nature were used to provide didactic tools for the prediction of global limits by interpreting the concept of Planetary Boundaries (Chapter 2). The newly developed RPCW model indicates that six of nine planetary boundaries are waste accumulation problems, offering a new perspective on the challenges we face in the Anthropocene. The model revealed the thresholds that exist in the shifting from a pristine world to a resource-limited world and finally to a waste-limited world. Technological development has led us to move from the pristine world, where there are only resources and no human consumption, through the resource-limited world, where the acquisition of resources by the consumer is limited by resource scarcity, and finally to a waste limited world, where the acquisition of resources by the consumer is limited by excessive waste accumulation. We are currently faced with a shift from a resource-limited world as classically described by Malthus, 1798 and the seminal work of the Club of Rome (Meadows et al., 1972), to a waste limited world. The optimal solution might be to find a balance between a resource-limited and a waste-limited world so that we can maintain human need and avoid the waste accumulation problems. This solution requires technological advancement in the waste treatment rate and the improvement of human consensus to avoid reckless consumption (Chen, 2004; Dauvergne, 2010). The transition to a waste-limited world is never more visible than in the current conflict between the maintenance of healthy ecosystems and human development, as waste generated by anthropogenic activities cannot be recycled to become a resource within human timescales. The results of my RPCW model serve as an inspirational message of the realization of the challenges faced by society in the Anthropocene.

Aquatic systems are clear examples of ecosystems under threat from anthropogenic 'waste' in the form of excessive fertilization (i.e., eutrophication). Here, consumer-resource interactions between phytoplankton abundance and nutrient loading informed the determination of nutrient thresholds by providing the mechanistic framework of a model, i.e., the GPLake model, that was derived to predict the load-response curve for lakes with variable characteristics (chapter 3). The relations defined by GPLake are based on the consumer-resource interaction of phytoplankton community with the limiting nutrient, i.e. P, and end up with the limitation by the light due to light extinction caused by massive phytoplankton abundance. Thus, the GPLake model defines the load-response curve of P loading and phytoplankton biomass, offering nutrient thresholds that can be used in eutrophication management. The mechanistic framework derived from the consumer-resource interaction model allows GPLake to be parameterized by data from lab, field and modelling studies. The results showed that the load-response curves parameterized from different data sources can be adjusted to a consistent pattern among the lab, field and modelling approaches when the same lake characteristics were applied. Consequently, the GPLake model has the potential to be used as the first estimation of chlorophyll-*a* production under varying P loads, and is applicable to a wide range of lakes with different characteristics due to its mechanistic basis.

GPLake-S further informed the prediction of the load-response curve by including both N and P (chapter 4) as limiting nutrients. Its mechanistic framework is derived from the consumer-resource interactions between multiple species and nutrients, including both N and P. Similarly to GPLake, the phytoplankton end up with the limitation by light at high nutrient loading due to overgrowth. Specific to the derivation of GPLake-S, is that it is necessary to make assumptions that lead to species co-existence. I simplified the model down to three phytoplankton species, based on the results that the resource competition of three species already captures 97% of the total phytoplankton biomass that would be attained with a large number of species. With the derivation of GPLake-S we have a model that captures the variability of phytoplankton community stoichiometry while being simple enough to be easily applicable in eutrophication management.

Finally, by expanding a complex process-based model, I studied consumer-resource interactions to explain how the biological traits of harmful algal specific cyanobacteria can alter a nutrient threshold, defined as nutrient loading threshold. The results in chapter 5 indicating that cyanobacteria can fortify the resilience of lakes to persist in a turbid state but hardly affect the resilience of lakes to maintain a clear state. For a turbid lake more nutrient reduction effort is needed for restoration when the cyanobacteria species have traits that regulate buoyancy or fix nitrogen. For a clear lake, those traits of cyanobacteria will not have an impact on nutrient loading threshold. This suggests that the policy-maker needs to consider the cyanobacterial traits when applying measures to reduce nutrients in deteriorated aquatic systems. The underlying mechanism can be explained in terms of the competitive traits that influence how cyanobacteria uptake nutrients. For example, buoyancy regulation and nitrogen fixation cause the consumer-resource interactions of cyanobacteria to have extra positive feedback loops compared with the cyanobacteria without such traits. Such insights into the importance of traits on nutrient limits are hard, if not impossible, to test in real world situations. Only through the application of process-based models we are able to derive scenarios where we can predict nutrient thresholds for eutrophication management in such detail, thereby giving valuable insights for policy and management.

6.2 Complexity of model formulation

Simulating all processes in nature and society is not possible due to the lack of understanding and knowledge, as well as computational limitations and data to validate such models (Purves et al., 2013). Therefore, concessions to the level of model complexity need to be made according to their purposes. In this thesis, the aim to derive the nutrient thresholds for the management of aquatic ecosystems is achieved with models with different levels of complexity. Each chapter puts forth consumer-resource interactions as the basis for model formulation and tailors the complexity to a level which corresponds to the purposes of the model (Figure 6.1).

The Verhulst model (Verhulst, 1845) and Tilman model (Tilman, 1982) used in chapter 2 define the basis of consumer-resource interaction and focus on the population itself and on the resource limitations, respectively. The newly developed RPCW model has expanded on consumer-resource interactions by two more elements, producer and waste. These two elements are essential for describing the consumer-resource interactions in the Anthropocene under the context of the increasing human activities and the consequences. In the global context, consumer-resource interactions describe the relations of human beings as consumers and the food, clean water, clothes, and other products as resources that consumers demand. As a result of the imbalance of high consumption rate and low waste cycling rate, waste accumulation becomes the major issue that threatens human sustainable development. For example, the greenhouse gas CO_2 in the atmosphere that causes global warming (Lashof et al., 1990) and the over enrichment of nutrients in aquatic ecosystems that cause harmful algal blooms (Hallegraeff, 2003) are both waste problems.

To determine the nutrient thresholds that help guide aquatic ecosystem restoration and conservation, consumer-resource interactions are used to derive the relations of nutrient loading and phytoplankton biomass. Specifically, the load-response curves addressed in chapter 3-5 are all derived based on the relations of nutrient loading and phytoplankton biomass at equilibrium. The difference between the three chapters lies in the complexity of model formulation. GPLake deals with a single nutrient resource, P, and the consumer as the phytoplankton community, including the effect of light. As one step further, we defined the consumer-resource interactions with two resources, N and P, in chapter 4. This is a valuable expansion of the model in light of the importance of N and colimitation by both P and N (see e.g. Lewis et al., 2020). Reducing both N and P loads to an aquatic system may not be equally feasible for management. Reducing N is considered more costly and the effect of reducing N may be insignificant because of the natural nitrification processes (Schindler et al., 2008). This is largely the reason why the traditional focus of eutrophication management has been on P reduction, which was reflected in early model development (Imboden, 1974; Vollenweider, 1975; Lung et al., 1976). However, the reduction of N can be equally important as P to control eutrophication because N is another essential nutrient for phytoplankton (Conley et al., 2009; Paerl et al., 2016b). Hence, I saw a need for the determination of the thresholds for both N and P in eutrophication management so that policy makers have a primary estimate of the effort required to restore their lake systems. GPLake-S fills that gap, as it can indicate whether the ecosystem is N limited or P limited so that policy makers can make fast first estimates of the effort needed for restoration prior to setting out on more in depth studies of their systems and more complex modelling exercises. The most complex model used in this thesis is the expanded PCLake+. We need this model to define more specific scenarios. Species-specific traits are among the important specific elements that can affect nutrient loading thresholds. This proves that consideration of influential ecological processes is important for policy makers to make accurate estimates. The models in this thesis deal with different level of complexity by capturing the fundamental mechanism of consumer-resource interactions with the necessary details depending on their purposes (Figure 6.1).

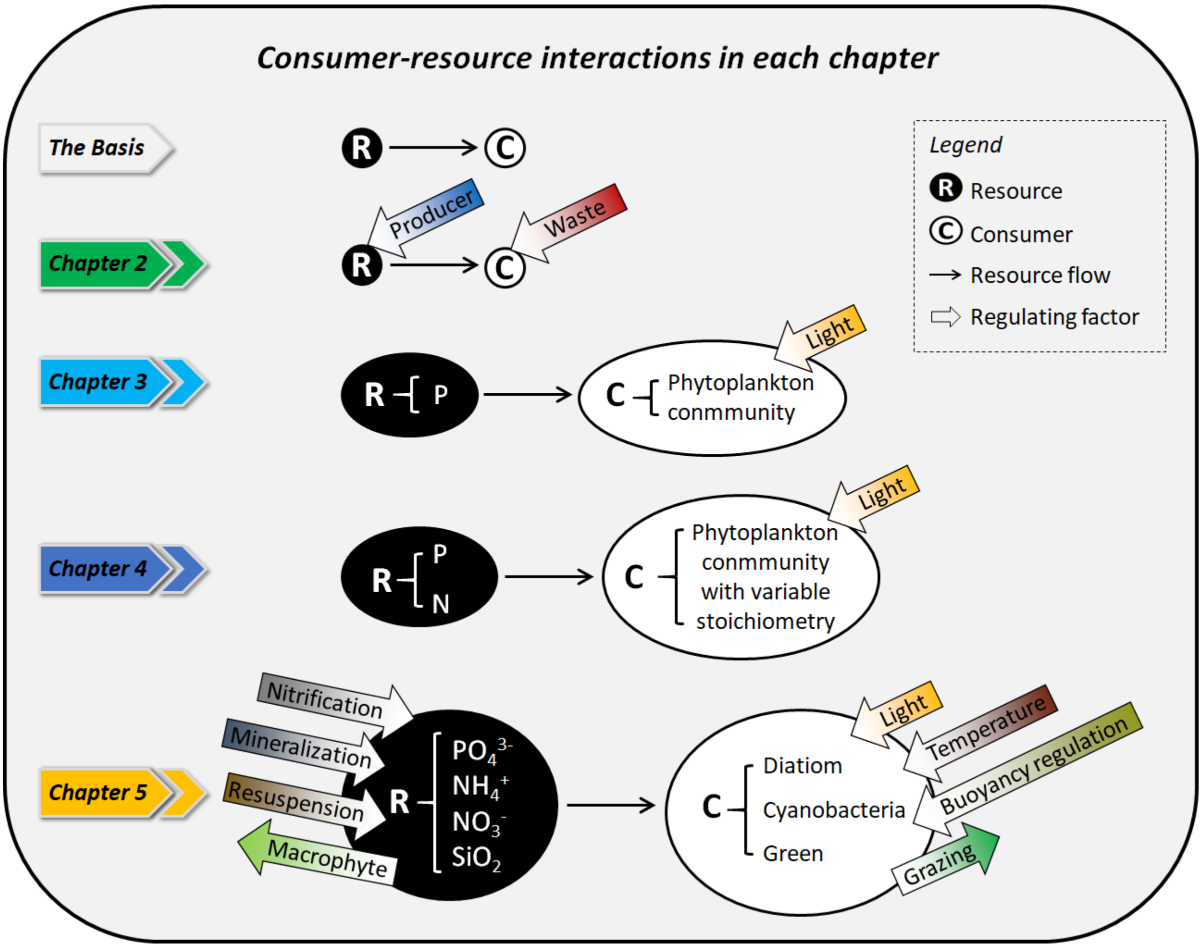

Figure 6.1 Model complexity in model formulation based on consumer-resource interactions defined in each chapter.

6.3 Complexity of model parameterization

In addition to the number of equations, model complexity is also reflected in the number of parameters that a model has. In this thesis, the RCWP model requires nine parameters, the GPLake model requires five parameters, the GPLake-S model requires eight parameters and the PCLake+ model has over five hundred parameters. Early eutrophication models (e.g. Vollenweider, 1968) were statistical models where parameters were dependent on the data set to which they were fitted and had little direct real world mechanistic interpretation. In contrast, all models presented in this thesis are mechanistic in their formulation. Therefore, of their parameters have clear, globally applicable definitions that translate to real world processes. Users can adjust the values of these parameters to fit their specific case. In fact, calibration of a model is often required as a vital first step when users want to apply a model to a certain case study (Gupta et al., 1998). Calibration is not a trivial task though. For example, in the simplest case of a statistical linear model, the parameters are dependent on the data set and have little to no real world meaning. For simple mechanistic models such as the Tilman and Huisman model, the parameters can be measured in laboratory experiments (Tilman, 1982; Huisman et al., 1994; 1995), but may be difficult to measure under field conditions. GPLake and GPLake-S have benefited from such a mechanistic framework based on consumer-resource interactions, but have been designed specifically with parameters in mind that have obvious meaning to empiricists. The parameters required to run GPLake and GPLake-S are the lake depth, residence time and nutrient loadings (P or both N and P). These parameters are easily translated to management practice in terms of their meaning and are relatively easy to measure. However, these input parameters can change among different aquatic ecosystems; hence the model can give different predictions. Policymakers can benefit from the low requirement of the input parameters to get to a first-order estimate of water quality and nutrient thresholds, and therefore give quick answers regarding the need and potential for management of a system. Therefore I think that GPLake and GPLake-S are suitable to provide a primary prediction for policy-makers to estimate the lake trophic conditions. This is similar to the function of a general practitioner (GP) who serves as a first gatekeeper to the medical system by estimating the severity of the illness of their patient. Such a gatekeeper model is important because the first estimation may influence the decision of whether the policy-maker will choose to invest further time and money on research and measures to improve the water quality. Lake depth, residence time and nutrient loading are key bits of data that are commonly collected in water management (Rast et al., 1978; Messager et al., 2016). The values of biological parameters such as the c_1 and c_2 for the GPLake model and the stoichiometric parameters for the GPLake-S model are hard to measure. Therefore, we parameterized them by data from lab, field and modelling studies based on their mechanistic framework and provided default values for the model users. Due to their simplicity and quick application, the GP models are well suited for consultants to facilitate interactive workshops together with managers and policy makers. Here the participants can receive near-instant estimates of the nutrient limits of their lake system, and the required effort needed to improve the water quality.

The RPCW model is also a simple mechanistic model with limited parameters. In contrast to the GPLake and GPLake-S models, the RPCW model uses conceptual parameters which fit its didactic purpose. Conceptual models are assemblages of assumptions and can inform the potential changes of a system that is hard to understand based on human intuition (Cuddington et al., 2013). The interpretation by the RPCW model for the concept of Planetary boundaries improves our understanding of the problems faced by society in the Anthropocene. Hence, the issue of parameter does not directly occur in the context of this chapter. The model may be used for practical predictions though, such as using the RPCW model to determine the nutrient limit of a lake system. To simulate eutrophication in an aquatic ecosystem, the resource can be identified by essential nutrients N and P, the production rate can be defined as the fertilizer production rate, the consumers are farmers, the waste is the nutrient discharge from farming. Here the occurrence of phytoplankton blooms would be a consequence of excess waste (i.e. eutrophication). However, to apply the RPCW model to such a question would require specific parameterization and calibration. This is in no way an easy task as the RPCW model is not a purely ecological model, but rather a social-ecological model where ecological and anthropogenic processes interact closely. While difficult to parameterize and validate, the relative simplicity of the RPCW model can serve as a stepping stone to link the ecosystem dynamics with social dynamics, a much needed step towards transdisciplinary integration (Angelstam et al., 2013; Mooij et al., 2019). With such a model we could simulate the feedback mechanisms where changing lake pollution can cause increasing social awareness and action to improve water quality (Janssen et al., 2019a; Mooij et al., 2019). Models of limited complexity in terms of their parameters are not without their downsides. There is a limit to what these simple models can deliver in terms of predictive power.

Models with many parameters, in contrast, are much more suited to scenario analyses and prediction of the impacts of management measures. PCLake+ for instance has over five hundred parameters that allow the user to make complex combinations suiting their scenario designs. Most of these biological parameters are dynamic and can change with the changing environment. For example, although the maximum growth rate of a species is a constant, the actual growth rate is affected by nutrient concentration, temperature and light. This dynamic nature of parameters differentiates ecological models from physical models such as Newton's second law of motion (Newton, 1687). Applied to the force of gravity, a model describing the force exerted by gravity on a body of a given mass is $F=mg$. F here is the force exerted on an object through gravity, m equals the mass of the object and g is the standard acceleration due to gravity. The parameter g is well known to be 9.81 m s^{-2}, and is largely unchanging through time and space on earth. Beyond the boundaries of system earth it takes on other values though; on the moon it has a value of 1.62 m s^{-2} because the moon has a different mass than the earth (di Prampero, 2000). Such a parameter is stable, certain and largely unchanging within the boundaries of a system. Ecological parameters, in contrast, are often not well known, and are dynamic within the confines of the system and thereby highly uncertain at any point in space or time. This leads to the uncertainty of the prediction of ecological models (Yates et al., 2018).

Further complicating ecological predictions is that, due to the multi-dimensional parameter space and the sheer number of parameters, it is highly unlikely that calibration datasets are sufficiently large to avoid overfitting. Overfitting of the model, makes its applicability beyond the calibration data limited, thereby reducing its capacity to make accurate predictions of conditions as yet unknown (Janse et al., 2010). Simple models can reduce this uncertainty through their limited number of parameters. Nonetheless, simple models can be less suitable to perform scenario analyses, as not all relevant processes relevant to a scenario are necessarily included. For example, buoyancy regulation of cyanobacteria is not part of the GPLake model, nor are cyanobacterial processes explicitly defined in GPLake. Therefore, a user cannot calculate the impact of management scenarios aimed at reducing buoyancy of cyanobacteria and its impact on bloom formation by using methods such as artificial mixing (Visser et al., 2016; Li et al., 2018), simply because such processes are not included in the model. Hence, the model would either have to be expanded, increasing its parameter complexity in the process, or a more complex model would be used (such as the PCLake+ model in chapter 5). Either option leads to an increase in parameter complexity and the problems inherent therein. Hence, I advocate the use of simple GPLake and GPLake-S as suitable models for the first estimation of nutrient limits for policymakers. After the decision is made to invest more time and energy into restoration, a PCLake+ type of the model, combined with in-depth measurements and data generation, can be very helpful in developing specific measures (e.g. fish removal (Janssen et al., 2019c), solid P sorbent application (Markelov et al., 2019) to manage aquatic ecosystems.

6.4 Complexity of models serving multiple roles

Beside model formulation and parameters, the application of models can present its own complexity (Murray, 2007). Mechanistic models have the advantage that they can make predictions of as yet unknown future conditions. Models can inform society on the possible outcomes of a wide range of topics, from economic declines to climate change, thereby allowing us to make different choices (see Lamperti et al., 2018). In the context of eutrophication management, these predictions are needed to determine the intensity of algal blooms and the conditions under which they will occur (Huang et al., 2018). Through these predictions we can estimate the seriousness of the problem and to see whether action is needed to mitigate or restore the water quality and safeguard much needed ecosystem services (Hallouin et al., 2018). Furthermore, models can help to assess different scenarios of management effort, and aid decision making aimed at nuisance mitigation with minimal disturbance to human activities. The application domain of models is not single sided, models serve multiple roles: 1) raise awareness for a the problem; 2) give first estimates of the severity of the problem; and 3) estimate effectiveness of action or inaction through scenario analyses. In my thesis, chapter 2 plays the first role, chapter 3 and 4 play the second role, and chapter 5 plays the third role.

A model designed for the application of raising awareness of an issue does not rely on its reflection of reality. Instead, the model requires clarity so that it is easily understood and can serve as a source of inspiration. Therefore, it needs to be a simple model that is easy to explain and understand, even if it does not reflect the complexity of the real world. An example of such a model can be found in the simple resource exhaustion model of the Club of Rome (limits to growth: Meadows et al., 1972). Despite not considering all ecological and societal processes, such a model in its relative simplicity has had a large impact on the understanding of the population limit on earth (Meadows et al., 1972). The IPCC climate model, on the other hand, is both complex and has had a big impact (Beck, 2011). This is supported by adequate monitoring of climate data and current atmospheric knowledge (e.g. Bernholdt et al., 2005). In an ideal world, where data is limitless and understanding of relevant processes exists, it makes sense to employ the most complex model available. Describing as many processes as possible will allow the most accurate and specific warnings for the future to be given. However, oftentimes such data and knowledge is limited or has uncertainties, and gathering it is both costly and time consuming, whereas there is a need to sound the alarm despite an incomplete picture of the future. Hence, more simplistic models are necessary, ideally striking a balance between data availability and complexity. Mechanistic models, incorporating existing theoretical knowledge in my opinion, meet this balance.

When the role of a model is to provide a first estimation of the severity of a problem, the model needs to be specific for the question that the users want to deal with. In the context of the medical gatekeeper, the GP will relate symptoms exhibited by a patient to possible diseases. This is why the Vollenweider type model is a good example of this, as it offers a direct link between symptoms (chlorophyll-*a*) to the 'disease' (P load), thereby offering a clear criterion for action.

This is why the Vollenweider model has had such a long-time appeal for policy makers. The model has gained international adoption and was brought up by the OECD meetings (Vollenweider, 1982). However, the diagnosis of a disease cannot leave out the individual characteristics of the patient. Similarly, the eutrophication problem is heterogeneous on a global scale (Carpenter, 2008). The resilience of aquatic ecosystems across the globe is locally specific, due to characteristics such as lake residence time, depth and local community composition (Janse et al., 1995). Hence, there is not a single planetary boundary but a collection of local boundaries that are sometimes exceeded and sometimes not. This is in stark contrast to the dynamics of CO_2, as the gas can be easily transferred uniformly around the world, and its effects are thus less subject to local conditions. Therefore, for the eutrophication of surface waters the challenge is to have a global view and keep in mind that the urgency of management can differ from site to site (Lürling et al., 2016). Hence, flexible models that include lake specific characteristics are necessary. This is the reason why, in this thesis, I propose that the consideration of the mechanism of consumer-interactions is a necessary pillar of models that make assessments of the severity of water quality issues.

For a patient with a medical condition, the step from diagnosis by the GP towards a specialized treatment plan requires a more thorough knowledge of the patient and the range of options available for treatment. Here, in the case of a waterbody with a eutrophication problem, complex models that require more elaborate input come into play, such as the PCLake+ model. These models, fed with more thorough analysis of existing data or through the collection of new data, can be used to make predictions of management measures and their efficacy for a given lake with its specific characteristics. Such a complex model is ill-suited to be used for a first estimation of the severity of a water quality issue because understanding the model is difficult and the calibration and validation of the model is time consuming and data intensive. However, this type of model is important for considering more detailed processes that are relevant in restoration efforts. With PCLake+, we can develop some practical scenarios such as mowing, removing the fish, dredging, and other measures to test whether these measures are effective to reach restoration goals (Janse et al., 1995; Mellios et al., 2015; Andersen et al., 2020). Such scenario studies cannot be performed in the same level of detail by the simple models. Therefore, these two types of models may be complementary, where the simpler models serve to inform on nutrient thresholds, and the complex models may then serve to calculate the explicit impacts of changes in social, technical or ecological configurations in the lake through management action.

One additional note is that all the roles of models that I have written about in my thesis take a view of reaching a long-term improvement in our ecosystems through management. There are also models that have neither of the roles of the models in my thesis, though that does not make them less important. For example, weather forecasting makes use of complex models. Such models are not understood by the general populace, yet have profound impact on their daily lives. Through the prediction result of whether it will be rainy, cloudy or sunny, decisions are made on mode of transportation (bike, car, train), or on holiday activities (stay home, go hiking). Here the complexity of the model is purposefully obfuscated from the casual user, making the prediction easy to understand. Such an approach does not fit into the roles of models I described in this thesis. This type of the model gets its credits from its sensitivity to time. The forecast of yesterday is not useful for your decision of tomorrow. For this type of model, the technique of data assimilation is important. The analogue for the context of eutrophication management is found in the prediction of algal blooms, used to inform people whether they can safely swim in a lake (see e.g. Ibelings et al., 2003). To date such predictions, however, are not yet at the level where they have the accuracy to compete with the weather forecast, though current advances in sensor technology and computer power should make this a reality in the near future (Bertone et al., 2018).

The chapters present in this thesis show a diversity in complexity and serve very different roles. Through this they are a good example of the importance and the benefits of model diversity (Janssen et al., 2015). Just like people playing different roles to keep society operational, models with different applications play their own role in a system and together they can help in the maintenance of good ecological states and serve to achieve sustainable development goals (Mooij et al., 2019).

6.5 Concluding remarks

To meet the sustainable development goals (SDGs) and avoid or reverse the anthropocenic damage done to our ecosystems and planet as a whole, drastic action is needed. In this thesis I have argued that basic mechanistic understanding, in the form of consumer-resource interaction theory, is needed to make good predictions of (nutrient) thresholds. These chapters provide a mechanistic framework for the load-response curve so that they are adaptive to the structural changes of systems (e.g. lake depths, changing community composition, new species traits). In this thesis I have presented four different models that are capable of predicting limits such as nutrient thresholds. Three of these models are newly developed within the context of this thesis. Using these, and other existing models I believe we can guide policy and management effectively towards a more sustainable world where targets are based on mechanistic knowledge of our ecosystems. For example, the RPCW model (chapter 2) can be used to show how reducing the consumption rate impacts global limits. From chapter 3 and 4, changing lake residence time can be simulated as the first estimate of the measures to improve water quality. From chapter 5, climate change scenarios can be simulated to see its effect on cyanobacterial traits that affect critical nutrient loadings. All these different models can help to set proper limits and develop measures aimed towards a sustainable Anthropocene. Models that are able to improve our understanding of the limits to human pollution are essential to safeguard a sustainable future. Together with my coauthors, I have developed models and modelling strategies of varying complexity that all serve this goal. Through such model diversity I hope to make a contribution to both science and society.

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Appendices

All appendices for this thesis are available online: https://drive.google.com/drive/folders/1UuAcKyN-HNaSVxn0Milt-Sxsnd7FZ0AI?usp=sharing. By this link you can find the following appendices:

Appendix 2.1	Branches of inquiry for the concept of Planetary Boundaries (published as supplementary material in Downing et al., 2020).
Appendix 2.2	Details on the dynamics and analyses of the new Resource-Producer-Consumer-Waste model (published as supplementary material in Downing et al., 2020).
Appendix 3.1	Derivation of the GPLake model based on Tilman's and Huisman's theory (published as supplementary material in Chang et al., 2019b).
Appendix 3.2	Sensitivity analysis of GPLake (published as supplementary material in Chang et al., 2019b).
Appendix 3.3	PCLake simulations for the default lake and lakes with different lake characteristics (published as supplementary material in Chang et al., 2019b).
Appendix 3.4	Uncertainty analyses of GPLake (published as supplementary material in Chang et al., 2019b).
Appendix 3.5	GPLake Tool (published as supplementary material in Chang et al., 2019b).
Appendix 3.6	Suggestions on how to extrapolate GPLake from lab scale to field scale in eutrophication management (published as supplementary material in Chang et al., 2019b).

Appendix 4.1	Overview of the four possible outcomes of the Tilman model of two species competing for two resources.
Appendix 4.2	Parameters used in the exploratory analysis to determine the number of species in GPLake-S.
Appendix 4.3	Field, experiment and model data on N:P ratios used to parameterize GPLake-S.
Appendix 4.4	Formulas to calculate the stoichiometric parameters of GPLake-S.
Appendix 4.5	Equations for the lines that specify at which levels of inflowing nutrients switches between types of limitations for phytoplankton abundance in GPLake-S occur.
Appendix 4.6	Comparison of some of the concepts and assumptions underlying GPLake-S and BLOOM II.
Appendix 4.7	GPLake-S Tool.
Appendix 5.1	Conversion in Parameters of Nitrogen Fixation (published as supplementary material in Chang et al., 2020).
Appendix 5.2	The R script for Bifurcation Analyses (published as supplementary material in Chang et al., 2020).
Appendix 5.3	The expanded PCLake+ (published as supplementary material in Chang et al., 2020).
Appendix 5.4	Supplementary Figures (published as supplementary material in Chang et al., 2020).

Summary (English)

The concept of Planetary Boundaries has called attention to the fact that there are major challenges that are threatening sustainable development of human society in the Anthropocene. Once the boundaries, or limits, on ecosystem sustainability are crossed, reversing the collapsed ecosystem back to a healthy ecosystem state that is suitable for human living can be rather difficult. Eutrophication in aquatic ecosystems is part of the Planetary Boundaries. Human activities such as agriculture, industrial production and domestic consumption discharge nutrients to aquatic ecosystems, causing severe deterioration of aquatic ecosystems when nutrient loading thresholds are exceeded. This deterioration is often accompanied by harmful algal blooms. The toxic algal blooms can threaten the safety of drinking water, and damage other organisms in the aquatic ecosystem through their shading of light or the depletion of oxygen during decomposition. **Chapter 1** of this thesis explains why the determination of nutrient thresholds is important for a sustainable Anthropocene and why I decided to use consumer-resource interactions as the basis to determine the nutrient thresholds.

Studies have shown that global inflows of N and P to many aquatic ecosystems are currently at the level that causes aquatic ecosystem functioning to collapse. As a result, many shallow aquatic ecosystems are experiencing a turbid state and have stopped providing essential ecosystem services. While there are still many aquatic ecosystems with transparent water, these are often located in areas where human population density is relatively low. To restore the turbid lakes to clear states and to maintain clear lakes with a good ecological state, the determination of nutrient limits for eutrophication management is essential. Determination of the nutrient limits, or thresholds, at which shifts to a eutrophic state can occur can help to maintain a healthy ecosystem in two ways. Once the nutrient thresholds are defined, we can use the thresholds as the reference for restoration, and also use it as the reference for conservation. For restoration, we need to reduce the nutrient loading below the threshold. For conservation, we need

to keep the nutrient loading under the threshold. These are not necessarily the same thresholds, e.g. shallow lakes often show hysteresis in response to changing nutrient loadings. While both efforts for restoration and conservation are challenging, determination of the limits itself is also challenging. Aquatic ecosystems comprise complex processes that are hard to be captured by the human mind. Modelling approaches are therefore necessary to help determine the limits. Besides, these thresholds are dynamic because of the variance of ecological processes among ecosystems and the changing environment by time. Nutrient thresholds are commonly determined based on load-response curves. This curve can have different shapes depending on the specific circumstances and the dynamics of external pressures such as nutrient loading. Therefore, mechanisms of ecological processes need to be considered in order to adapt to the changing environmental conditions and human activities.

In this thesis, I used consumer-resource interactions as the mechanistic basis of the relations between nutrient loading and phytoplankton biomass to interpret, derive and analyze nutrient thresholds for eutrophication management. Consumer-resource theory covers a broad spectrum of topics that all go to the heart of ecology because of its focus on providing a mechanistic interpretation of the interactions of organisms with each other, and with their environment, and the emergent dynamics that stem from these interactions. In practice, the global limits defined by the concept of Planetary Boundaries are interpreted in **chapter 2** by two seminal and one newly developed consumer-resource models that represent the interactions between human beings and nature. Here, the seminal models by Verhulst and Tilman are used to define the limits for human society in terms of maximum population size, maximum rates of resource exploitation and required rates of waste treatment to balance rates of exploitation. To this purpose, I added two elements to the Tilman style consumer-resource model, namely producers and waste, resulting in the newly developed RPCW model. An interesting outcome of analysis with this model is that six of the nine Planetary Boundaries turned out to be waste accumulation problems, offering a new perspective on the challenges we face in the Anthropocene. The RPCW model conceptually defines the thresholds of the shift from a pristine world to a resource-limited world and finally to a waste-limited world. It indicates that technological development has brought us away from the pristine world, where resources were effectively unlimited and early humans did not have a significant impact on the environment, through the resource-limited world, where the acquisition of resources by the consumer was limited by resource scarcity, and finally to a waste limited world, where the acquisition of resources by the consumer is limited by excessive waste accumulation. The transition to a waste limited world is clearly visible in the current conflict between the maintenance of healthy ecosystems and human development, as much of the waste generated by anthropogenic activities cannot be recycled to become a resource within human timescales. The optimal solution might be to find a balance between a resource-limited and a waste-limited world so that in the words of Kate Raworth we can "meet the needs of all within the means of the planet". This solution requires technological advancement aiming for the improvement of the waste treatment rate, the improvement of human awareness of environmental problems, and decisive action to avoid reckless consumption. The work presented in this chapter serves as a didactic tool to deliver an inspirational message for addressing the challenges faced by society in the Anthropocene.

From there, I move the focus from the broad scope of global limits to the nutrient limits, or thresholds, in aquatic ecosystems. Identification of nutrient thresholds is important to help estimate the degree to which nutrient loadings in eutrophic waterbodies should be reduced and not be surpassed for restoration and conservation, respectively. I derived two models based on consumer-resource interactions to predict the load-response curve between phytoplankton abundance and nutrient loading and to determine nutrient thresholds across lakes with a spectrum of characteristics. The GPLake model derived in **chapter 3** is based on the consumer-resource interaction of a phytoplankton community under phosphorous and light limitation. The mechanistic framework derived from the consumer-resource interaction model allows GPLake to be parameterized by data from lab, field and modelling studies. The results showed that the load-response curves parameterized from different data sources could be adjusted to a comparable pattern among the lab, field and modelling approaches when the same lake characteristics were applied. Consequently, the GPLake model has the potential to provide the first estimation of chlorophyll-*a* production under varying P loads and is applicable to a wide range of lakes with different characteristics due to its mechanistic basis. It can therefore play a role comparable to a 'General Practitioner' in the medical world, namely to provide a first diagnosis of what is needed to come to a healthy system and make suggestions on where to look for more specialized advice.

To add the essential nutrient of N in the load-response curve, I derive from GPLake another model called GPLake-S that formulates the abundance of phytoplankton community and nutrient loadings of both N and P in **chapter 4**. The derivation of this model is based on the consumer-resource theory by Tilman of multiple species competing for two essential nutrients, i.e. N and P. Similarly to GPLake, the phytoplankton become limited by light at high nutrient loading due to overgrowth. In deriving the equations of GPLake-S I make the assumption that natural communities of phytoplankton comprise many species that have the potential to coexist if nutrients are supplied at ratios that match their requirements. I simplified the model according to the results that the resource competition of three species can mostly capture the results of phytoplankton biomass with a large number of species. With the derivation of GPLake-S we have a model that captures the variability of phytoplankton community stoichiometry while being simple enough to be easily applicable in eutrophication management.

Finally, I expanded the complex process-based model PCLake+ to study how specific biological traits of cyanobacteria influence their consumer-resource interactions and alter nutrient loading thresholds in **chapter 5**. The results indicate that cyanobacteria can strengthen the resilience of lakes to persist in a turbid state but hardly affect the resilience of lakes to maintain a clear state. For a turbid lake more nutrient load reduction effort is needed when the cyanobacteria species have traits that regulate buoyancy or fix nitrogen. For a clear lake, the traits of cyanobacteria will not have an impact on the nutrient loading threshold. This suggests that policy-makers need to consider the cyanobacterial traits when applying measures to reduce nutrients in deteriorated aquatic systems. The underlying mechanism is that the cyanobacteria's competitive traits influence how they take up nutrients. For example, buoyancy regulation and nitrogen fixation result in extra positive feedback loops in the consumer-resource interactions of those species that have such traits compared with the cyanobacteria without such traits. Such insights into the importance of traits on nutrient limits are hard, if not impossible, to test in real world situations. Only through the application of process-based models are we able to derive scenarios where we can predict nutrient thresholds for eutrophication management in such detail, thereby giving valuable insights for policy and management.

Taking stock of the models that I developed, I asked myself how each of these models can be used separately, or in association, to contribute to a sustainable Anthropocene in **chapter 6**. By focusing on the complexity of the model formulation, parameterization, and application, I explain the similarities, differences and complementarities of the models I derived in this thesis, and describe their different roles in eutrophication management. While rooted in consumer-resource theory and differing enormously in the level of complexity in which they describe the system under study, each of these models serves the purpose to determine thresholds in human impact on the environment. Producer and waste are two essential elements constructed in the RPCW model to point out the waste problem in the Anthropocene. It has few parameters and is easy to understand; therefore it is suitable to be used as an didactic tool to raise the awareness of the public of eutrophication as a severe waste problem due to excessive human activities. For this type of conceptual model, the values of the parameters do not necessarily have to be defined realistically, as long as it can be applied to deliver a message. Models with an equally simple structure, such as

GPLake and GPLake-S, but with a realistic parametrization based on field, lab and model data can be used as first estimation tools in real case studies on eutrophied aquatic ecosystems. Due to their simplicity and quick application, the GPLake and GPLake-S models are suited for consultants to facilitate interactive workshops together with managers and policy makers. Finally, the complex model PCLake+, which was developed and tested in practice over many decades, is suitable for scenario studies. This complex model that covers many specific ecological processes can be used to determine nutrient thresholds under a wide range of management scenarios for ecosystem conservation and recovery.

I see value in the diversity of the models that I developed for achieving a sustainable Anthropocene by raising the awareness of people, supporting knowledge-based decision making by policy makers, and providing cost-effective measures for eutrophication management by water quality managers.

Lastly, I want to emphasize my personal philosophy that underlies my work. Foremost, the future can be challenging, and we need the power of science to face it. By the power of science I mean knowledge and rational thinking. Science provides approaches to understand the world, for example by studying both natural and social systems. By this power, we can observe, predict and change our limits. *In my view it is essential to know the limits for nature, society and ourselves to achieve a sustainable Anthropocene.* In this thesis I focused on how to determine limits to human exploitation of the environment, using mathematical models. Mathematics is commonly regarded as theoretical and difficult to understand, but the hypotheses and messages delivered by mathematical equations are solid and beautiful. Looking ahead, I think that models that include social-ecological interactions can play an important role in achieving a sustainable Anthropocene. For example, one important social-ecological perspective that I think should be communicated more is that, although restoration and conservation of ecosystems have economic cost, the collapse of ecosystem functions will have a much bigger economic cost. Once this awareness of external costs is settled in the minds of people, policy can change to support a sustainable Anthropocene.

Summary (Nederlands)

Het concept van “Planetaire Grenzen” heeft de aandacht gevestigd op het feit dat er grote uitdagingen zijn die een duurzame ontwikkeling van de menselijke samenleving in het Antropoceen bedreigen. Zodra de grenzen, of limieten, van de draagkracht van ecosystemen zijn overschreden, kan het moeilijk zijn om het ingestorte ecosysteem terug te brengen naar een gezonde toestand die een geschikte leefomgeving voor de mens biedt. Eutrofiëring in aquatische ecosystemen maakt deel uit van de Planetaire Grenzen. Menselijke activiteiten zoals landbouw, industriële productie en huishoudelijk gebruik lozen voedingsstoffen oftewel nutriënten in aquatische ecosystemen, waardoor aquatische ecosystemen ernstig worden aangetast wanneer de drempelwaardes voor nutriëntenbelasting worden overschreden. Deze achteruitgang gaat vaak gepaard met schadelijke algenbloei. De giftige algenbloei kan drinkwaterveiligheid bedreigen en andere organismen in het aquatische ecosysteem nadeling beinvloeden door beschaduwing of zuurstofuitputting door afbraakprocessen. **Hoofdstuk 1** van dit proefschrift legt uit waarom het bepalen drempelwaardes voor nutriënten belangrijk is voor een duurzaam Antropoceen en waarom ik besloot om consument-hulpbron interacties als basis te gebruiken om deze drempelwaardes te bepalen.

Onderzoek heeft aangetoond dat de wereldwijde instroom van stikstof (N) en fosfaat (P) naar veel aquatische ecosystemen momenteel op het niveau ligt waarbij het functioneren van deze ecosystemen zal instorten. Als gevolg hiervan bevinden veel ondiepe aquatische ecosystemen zich in een troebele toestand en leveren ze essentiële ecosysteemdiensten niet meer. Hoewel er nog steeds veel aquatische ecosystemen zijn met helder water, bevinden deze zich vaak in gebieden waar de bevolkingsdichtheid relatief laag is. Om de troebele meren te herstellen tot de heldere toestand en om heldere meren met een goede ecologische toestand te behouden, is het bepalen van grenzen aan de toelaatbare nutriëntbelasting voor de bestrijding van eutrofiëring essentieel. Het bepalen van deze nutriëntgrenzen, of -drempelwaardes, waarbij verschuivingen naar een eutrofe toestand kunnen optreden, kan op twee manieren helpen om een gezond ecosysteem in stand te houden. Zodra de nutriëntendrempelwaardes zijn gedefinieerd, kunnen we de drempelwaardes gebruiken als referentie voor herstel, en als referentie voor behoud van ecosystemen. Voor herstel moeten we de nutriëntenbelasting tot onder de drempelwaarde verlagen. Voor het behoud moeten we de nutriëntenbelasting onder de drempelwaarde houden. Dit zijn niet noodzakelijk dezelfde drempelwaardes, b.v. ondiepe meren vertonen vaak hysterese als reactie op veranderende nutriëntenbelasting. Hoewel beide inspanningen voor herstel en behoud uitdagend zijn, is het bepalen van de limieten zelf ook een uitdaging. Aquatische ecosystemen omvatten complexe processen die moeilijk te begrijpen zijn voor de menselijke geest. Modelbenaderingen zijn daarom nodig om te helpen de limieten te bepalen. Bovendien zijn deze drempelwaardes dynamisch vanwege verschillen in ecologische processen tussen ecosystemen en het feit dat de omgeving met de tijd verandert. Nutriëntendrempelwaardes worden over het algemeen bepaald op basis van dosis-responsrelaties. Deze relaties kunnen verschillende vormen hebben, afhankelijk van de specifieke omstandigheden en de dynamiek van externe drukfactoren zoals nutriëntenbelasting. Daarom moeten ecologische processen mechanistisch beschouwd worden om de relaties aan te passen aan de veranderende omgevingsomstandigheden en menselijke activiteiten.

In dit proefschrift heb ik de interacties tussen consumenten en hun hulpbronnen gebruikt als de mechanistische basis van de relaties tussen nutriëntenbelasting en fytoplanktonbiomassa om nutriëntendrempelwaardes voor eutrofiëringsbeheer te interpreteren, af te leiden en te analyseren. Theorie van consument-hulpbron interacties omvat een breed spectrum van onderwerpen die allemaal de kern van de ecologie raken vanwege de focus op het bieden van een mechanistische interpretatie van de interacties van organismen met elkaar en met hun omgeving, en de emergente dynamiek die voortvloeit uit deze interacties. In de praktijk worden de wereldwijde limieten, zoals gedefinieerd door het concept van Planetaire Grenzen, in **hoofdstuk 2** geïnterpreteerd door twee baanbrekende en één nieuw ontwikkelde consument-hulpbron-modellen die de interacties tussen mens en natuur vertegenwoordigen. Hierbij worden de baanbrekende modellen van Verhulst en Tilman gebruikt om de grenzen voor de menselijke samenleving te definiëren in termen van maximale populatiegrootte, maximale hulpbron exploitatiegraad en vereiste afvalverwerkingssneldheid nodig om de exploitatiegraad in evenwicht te brengen. Hiervoor heb ik twee elementen toegevoegd aan het Tilman-stijl consument-hulpbron-model, namelijk producenten en afval, resulterend in het nieuw ontwikkelde RPCW-model. Een interessante uitkomst van een analyse met dit model is dat zes van de negen Planetaire Grenzen afvalaccumulatieproblemen bleken te zijn, wat een nieuw perspectief biedt op de uitdagingen waarmee we in het Antropoceen worden geconfronteerd. Het RPCW-model definieert conceptueel de drempelwaardes van de verschuiving van een ongerepte wereld naar een wereld met beperkte hulpbronnen en uiteindelijk naar een wereld die beperkt wordt door afval. Het geeft aan dat technologische ontwikkeling ons heeft weggeleid uit de ongerepte wereld, waar de hulpbronnen in feite onbeperkt waren en de eerste mensen geen significante impact op het milieu hadden, via de wereld met beperkte hulpbronnen, waar de verwerving van hulpbronnen door de consument beperkt werd door schaarste van hulpbronnen, en tenslotte naar een wereld waarin afval beperkend is, waar de verwerving van hulpbronnen door de consument beperkt wordt door buitensporige afvalaccumulatie. De transitie naar een wereld waarin afval beperkend is, is duidelijk zichtbaar in het huidige conflict tussen het behoud van gezonde ecosystemen en menselijke ontwikkeling, aangezien veel van het afval dat wordt gegenereerd door menselijke activiteiten niet binnen menselijke tijdschalen kan worden gerecycled om opnieuw een hulpbron te worden. De optimale oplossing zou kunnen zijn om een balans te vinden tussen een wereld met beperkte hulpbronnen en een wereld beperkt door afval, zodat we, in de woorden van Kate Raworth, "in de behoeften van iedereen kunnen voorzien met de middelen die de planeet biedt". Deze oplossing vereist technologische vooruitgang die gericht is op de verbetering van de afvalverwerkingssnelheid, de verbetering van het menselijk bewustzijn van milieuproblemen en doortastende maatregelen om roekeloze consumptie te voorkomen. Het werk dat in dit hoofdstuk wordt gepresenteerd, is bedoeld als een didactisch hulpmiddel om een inspirerende boodschap over te brengen voor het aanpakken van de uitdagingen waarmee de samenleving in het Antropoceen wordt geconfronteerd.

Van daaruit verschuif ik de focus van de brede reikwijdte van wereldwijde limieten naar de nutriëntenlimieten, of -drempelwaardes, in aquatische ecosystemen. De identificatie van nutriëntendrempelwaardes is belangrijk om te helpen inschatten in welke mate de nutriëntenbelasting in eutrofe waterlichamen moet worden verminderd en niet moet worden overschreden voor, respectievelijk, herstel en behoud van ecosystemen. Ik heb twee modellen afgeleid op basis van interacties tussen consumenten en hulpbronnen om de belasting-reactie-curve tussen fytoplankton-abundantie en nutriëntenbelasting te voorspellen en om nutriëntendrempelwaardes te bepalen in meren met een scala aan kenmerken. Het GPLake-model dat is afgeleid in **hoofdstuk 3** is gebaseerd op de consument-hulpbron interactie van een fytoplanktongemeenschap onder fosfor- en lichtbeperking. Dankzij het mechanistische raamwerk dat is afgeleid van consument-hulpbron interactie modellen, kan GPLake worden geparametriseerd door gegevens uit laboratorium-, veld- en modelleringsstudies. De resultaten toonden aan dat de dosis-responsrelaties, geparametriseerd vanuit verschillende gegevensbronnen, een vergelijkbaar patroon tussen de laboratorium-, veld- en modelleringsbenaderingen gaan tonen wanneer deze toegepast werden op meren met dezelfde kenmerken. Dientengevolge heeft het GPLake-model de potentie om een eerste inschatting te geven van de chlorofyl-a-productie onder variërende P-belastingen en is het toepasbaar op een breed scala aan meren met verschillende kenmerken vanwege zijn mechanistische basis. Het kan daarom een rol spelen die vergelijkbaar is met een huisarts (in het Engels ‘GP’) in de medische wereld, namelijk om een eerste diagnose te stellen van wat er nodig is om tot een gezond systeem te komen en suggesties te doen waar je meer gespecialiseerd advies kunt zoeken.

Om het essentiële nutriënt N toe te voegen aan de dosis-responsrelatie, leid ik in **hoofdstuk 4** een ander model van GPLake af, genaamd GPLake-S, dat de fytoplanktongemeenschap-abundantie en nutriëntenbelastingen van zowel N als P beschouwd. De afleiding van dit model is gebaseerd op de consument-hulpbron theorie van Tilman van meerdere soorten die strijden om twee essentiële nutriënten, namelijk N en P. Net als bij GPLake wordt het fytoplankton beperkt door licht bij een hoge nutriëntenbelasting als gevolg van zelfbeschaduwing. Bij het afleiden van de vergelijkingen van GPLake-S ga ik ervan uit dat natuurlijke gemeenschappen van fytoplankton veel soorten omvatten die de potentie hebben om naast elkaar te bestaan als nutriënten worden geleverd in verhoudingen die overeenkomen met hun vereisten. Ik heb het model vereenvoudigd op basis van de resultaten dat de concurrentie om hulpbronnen van drie soorten in belangrijke mate de resultaten van fytoplanktonbiomassa met een groot aantal soorten beschrijven. Met de afleiding van GPLake-S hebben we een model dat de variabiliteit van de stoichiometrie van de fytoplanktongemeenschap vangt, terwijl het eenvoudig genoeg is om gemakkelijk toepasbaar te zijn in het beheer van eutrofiëring.

Ten slotte heb ik in **hoofdstuk 5** het complexe proces-gebaseerde model PCLake+ uitgebreid om te bestuderen hoe specifieke biologische eigenschappen van blauwalgen de consument-hulpbron interacties ervan beïnvloeden en de drempelwaardes in nutriëntenbelasting veranderen. De resultaten geven aan dat blauwalgen de weerbaarheid van meren kunnen versterken om in een troebele toestand te blijven, maar ze hebben nauwelijks invloed op de veerkracht van meren om een heldere toestand te behouden. Voor een troebel meer is meer inspanning nodig om de nutriëntenbelasting te verminderen wanneer de blauwalgsoorten eigenschappen hebben die het drijfvermogen reguleren of stikstof binden. Voor een helder meer hebben de eigenschappen van blauwalgen geen invloed op de drempelwaardes voor nutriëntenbelasting. Dit suggereert dat beleidsmakers rekening moeten houden met deze blauwalg-eigenschappen bij het toepassen van maatregelen om nutriëntconcentraties te verminderen in verslechterde aquatische systemen. Het onderliggende mechanisme is dat de competitieve eigenschappen van de blauwalgen invloed hebben op hoe ze nutriënten opnemen. Regulatie van het drijfvermogen en stikstoffixatie resulteren bijvoorbeeld in extra zelfversterkende terugkoppelingen in de consument-hulpbron interacties van die soorten die dergelijke eigenschappen hebben ten opzichte van de blauwalgen zonder dergelijke eigenschappen. Dergelijke inzichten in het belang van soortseigenschappen voor nutriëntendrempelwaardes zijn moeilijk, zo niet onmogelijk, te testen in situaties in de echte wereld. Alleen door de toepassing van proces-gebaseerde modellen zijn we in staat scenario's af te leiden waarin we nutriëntendrempelwaarden voor eutrofiëringbeheer zo gedetailleerd kunnen voorspellen, dat we waardevolle inzichten kunnen genereren voor beleid en beheer.

Bij het inventariseren van de modellen die ik ontwikkelde, vraag ik me in **hoofdstuk 6** af hoe elk van deze modellen afzonderlijk, of in samenhang, kunnen worden gebruikt om bij te dragen aan een duurzaam Antropoceen. Door te focussen op de complexiteit van de modelformulering, parametrisering, en toepassing, leg ik de overeenkomsten, verschillen en complementariteit uit van de modellen die ik in dit proefschrift heb afgeleid, en beschrijf hun verschillende rollen in eutrofiëringsbeheer. Hoewel ze geworteld zijn in de theorie van consumenthulpbron interacties en enorm verschillen in het niveau van complexiteit waarin ze het onderzochte systeem beschrijven, heeft elk van deze modellen tot doel om drempelwaardes te bepalen voor de menselijke impact op het milieu. Producenten en afval zijn twee essentiële elementen die in het RPCW-model zijn ingebouwd om op het afvalprobleem in het Antropoceen te wijzen. Het RPCW-model heeft weinig parameters en is gemakkelijk te begrijpen; daarom is het geschikt om te worden gebruikt als een didactisch instrument om het publiek bewust te maken van eutrofiëring als een ernstig afvalprobleem als gevolg van buitensporige menselijke activiteiten. Voor dit type conceptueel model hoeven de waarden van de parameters niet noodzakelijk realistisch te worden gedefinieerd, zolang ze maar kunnen worden toegepast om een boodschap over te brengen. Modellen met een al even eenvoudige structuur, zoals GPLake en GPLake-S, maar met een realistische parametrisering op basis van veld-, laboratorium- en modelgegevens, kunnen worden gebruikt als eerste schattingsinstrumenten in een echte casus over geëutrofieerde aquatische ecosystemen. Door hun eenvoud en snelle toepassing zijn de GPLake- en GPLake-S-modellen geschikt voor consultants om interactieve workshops te faciliteren samen met managers en beleidsmakers. Ten slotte is het complexe model PCLake+, dat decennia lang in de praktijk is ontwikkeld en getest, geschikt voor scenariostudies. Dit complexe model dat veel specifieke ecologische processen bestrijkt, kan worden gebruikt om nutriëntendrempelwaardes te bepalen onder een breed scala aan beheer-scenario's voor behoud en herstel van ecosystemen.

Ik zie waarde in de diversiteit van de modellen die ik heb ontwikkeld om een duurzaam Antropoceen te bereiken door het bewustzijn van mensen te vergroten, op kennis gebaseerde besluitvorming door beleidsmakers te ondersteunen en door kosteneffectieve maatregelen te bieden voor eutrofiëringsbeheer door waterkwaliteitsbeheerders.

Ten slotte wil ik de nadruk leggen op mijn persoonlijke filosofie die aan mijn werk ten grondslag ligt. In de eerste plaats kan de toekomst een uitdaging zijn, en we hebben de kracht van de wetenschap nodig om die onder ogen te zien. Met de kracht van wetenschap bedoel ik kennis en rationeel denken. De wetenschap biedt benaderingen om de wereld te begrijpen, bijvoorbeeld door zowel natuurlijke als sociale systemen te bestuderen. Door deze kracht kunnen we onze grenzen observeren, voorspellen en veranderen. *In mijn ogen is het essentieel om de grenzen van de natuur, de samenleving en onszelf te kennen om tot een duurzaam Antropoceen te komen.* In dit proefschrift heb ik me gericht op hoe grenzen te bepalen voor de menselijke uitbuiting van het milieu, met behulp van wiskundige modellen. Wiskunde wordt over het algemeen beschouwd als theoretisch en moeilijk te begrijpen vakgebied, maar de hypothesen en boodschappen die uit wiskundige vergelijkingen volgen, zijn solide en mooi. Vooruitkijkend denk ik dat modellen die sociaal-ecologische interacties bevatten, een belangrijke rol kunnen spelen bij het bereiken van een duurzaam Antropoceen. Een belangrijk sociaal-ecologisch perspectief dat naar mijn mening meer gecommuniceerd dient te worden, is bijvoorbeeld dat, hoewel herstel en instandhouding van ecosystemen economische kosten met zich meebrengt, de ineenstorting van ecosysteemfuncties veel grotere economische kosten zal hebben. Zodra dit besef van externe kosten in de hoofden van mensen is geworteld, kan het beleid veranderen om een duurzaam Antropoceen te ondersteunen.

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About the author

Manqi Chang, born on 19 March 1991, grew up in the city of Zhengzhou, one of the busiest transportation hubs in China. With her enthusiasm for nature and the willingness to become an engineer, Manqi started her undergraduate study in Water Conservancy and Hydropower Engineering at Hohai University in Nanjing, China, and focused her study on mechanics and hydrodynamics aiming for flood prevention and hydropower. Besides undergraduate study, Manqi kept active in extracurricular life working as a student leader of the university's Foreign Exchange Association and the photographer of the college newspaper during her undergraduate years. In 2013, she continued her master's study at Hohai University, with the focus shifted to water quality management using hydrodynamic measures. In that period, the idea of further studying ecology came to mind because of her ardent love and curiosity for nature. To make this reality, she applied and started the PhD at the Netherlands Institute of Ecology (NIOO-KNAW) in the Netherlands in 2016 and subsequently got a scholarship from China Scholarship Council (CSC). During her PhD, she worked as a model developer of aquatic ecosystems, focusing on mechanistic models based on ecological consumer-resource theory that range from simple didactic models through diagnostic models to complex ecosystem models. She developed a didactic Resource-Producer-Consumer-Waste model for understanding Planeray Boundaries within the context of sustainable development and the diagnostic and generically parameterized GPLake model for eutrophication management. Moreover, she extended the complex ecosystem model PCLake enabling it to simulate the floating process of cyanobacteria. Her work has been presented at multiple conferences and published in peer-reviewed scientific journals, and altogether in this thesis "Know your limits: Modelling consumer-resource interactions to derive nutrient thresholds for a sustainable Anthropocene".

Publications

Chang, M., Teurlincx, S., DeAngelis, D.L., Janse, J.H., Troost, T.A., van Wijk, D., Mooij, W.M., Janssen, A.B.G. (2019) A Generically Parameterized model of Lake eutrophication (GPLake) that links field-, lab- and model-based knowledge. ***Science of The Total Environment***. 695, 133887.

Chang, M., Teurlincx, S., Janse, J.H., Paerl, H.W., Mooij W.M., Janssen, A.B.G. (2020) Exploring how Cyanobacterial Traits Affect Critical Nutrient Loading in Shallow Lakes: A Modelling Approach. ***Water***. 12, 2467.

Downing, A.S.; **Chang, M.**; Kuiper, J.J.; Campenni, M.; Hayha, T.; Cornell, S.; Svedin, U.; Mooij, W.M. Learning from generations of sustainability concepts. (2020) ***Environmental Research Letters***. 15,8.

Gillefalk, M., Mooij, W.M., Teurlincx, S., Janssen, A.B.G., Janse, J.H., **Chang, M.,** Köhler, J., Hilt, S. (2019) Modelling induced bank filtration effects on freshwater ecosystems to ensure sustainable drinking water production. ***Water Research***. 157, 19-29.

Janssen, A.B.G., Janse, J.H., Beusen, A.H.W., **Chang, M.**, Harrison, J.A., Huttunen, I., Kong, X., Rost, J., Teurlincx, S., Troost, T.A., van Wijk, D. and Mooij, W.M. (2019) How to model algal blooms in any lake on earth. ***Current Opinion in Environmental Sustainability***. 36, 1-10.

Mooij, W.M., van Wijk, D., Beusen, A.H.W., Brederveld, R.J., **Chang, M.**, Cobben, M.M.P., DeAngelis, D.L., Downing, A.S., Green, P., Gsell, A.S., Huttunen, I., Janse, J.H., Janssen, A.B.G., Hengeveld, G.M., Kong, X., Kramer, L., Kuiper, J.J., Langan, S.J., Nolet, B.A., Nuijten, R.J.M., Strokal, M., Troost, T.A., van Dam, A.A. and Teurlincx, S. (2019) Modeling water quality in the Anthropocene: directions for the next-generation aquatic ecosystem models. ***Current Opinion in Environmental Sustainability***. 36, 85-95.

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Downing, A.S., **Chang, M.**, Collste, D., Cornell, S., Kuiper, J.J., Mooij, W.M., Svedin, U., van Wijk, D. (2020) Choosing inclusive futures for human development in the Anthropocene. ***Human Development Report 2020*** – *The next frontier: Human development and the Anthropocene* (Box 1.3, page 37). United Nations Development Programme.

Downing, A.S., **Chang, M.**, Collste, D., Cornell, S., Kuiper, J.J., Mooij, W.M., Svedin, U., van Wijk, D. (2020) Learning from sustainability science to guide sustainable human development. ***Human Development Report 2020 –*** *The next frontier: Human development and the Anthropocene* (Spotlight 1.1, page 94-98). United Nations Development Programme.

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (4.5 ECTS)

- Ensemble modelling of coupled hydrodynamic and biogeochemical processes to predict algal blooms in polluted lakes

Postgraduate courses (9.6 ECTS)

- GIS in practice; PE&RC (2016)
- Bayesian statistics; PE&RC (2017)
- Statistical uncertainty analysis of dynamic models; SENSE (2017)
- Consumer-resource Interactions; PE&RC (2018)
- Linking community and ecosystem dynamics; PE&RC (2018)
- Resilience of living systems; WIAS (2018)

Laboratory training and working visits (4.7 ECTS)

- Collaboration with PCLake; IGB, Berlin (2017)
- Learning BLOOM II; Deltares (2018)

Invited review of (unpublished) journal manuscript (3 ECTS)

- Water Research: nutrient limitation of phytoplankton in Chesapeake Bay: development of an empirical approach for water-quality management
- Hydrobiologia: water depth as the key controlling regulator associated with nutrient and gross primary productivity changes in a large floodplain-lake system
- Limnologica: nature favours “one” as the leading digit in phytoplankton abundance data

Competence strengthening / skills courses (2.8 ECTS)

- Scientific writing; WGS (2017)
- Presenting with impact; WGS (2019)

Scientific integrity/ethics in science activities (0.3 ECTS)

- Workshop during research day; NIOO (2017)
- Workshop as part of theme meetings; NIOO (2018)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.8 ECTS)

- PE&RC Day (2016)
- PE&RC First years weekend (2017)
- PE&RC Last years weekend (2020)

Discussion groups / local seminars / other scientific meetings (11.9 ECTS)

- Literature discussion of AqE; NIOO (2016-2020)
- NAEM (2017, 2018, 2020)
- Global change theme meeting; NIOO (2018-2020)
- Modelling and simulation discussion group; NIOO (2019-2020)

International symposia, workshops and conferences (10.9 ECTS)

- Global Water Quality Modelling Workshop; Wageningen, the Netherlands (2017)
- SIL; Nanjing, China (2018)
- Water Science for Impact; Wageningen, the Netherlands (2018)
- GLEON21; Muskoka, Canada (2019)
- ESP10; Hannover, Germany (2019)

Lecturing / supervision of practicals / tutorials (4.5 ECTS)

- Models for ecological systems (2018, 2019)

Colophon

The research presented in this thesis was conducted at the department of Aquatic Ecology at the Netherlands Institute of Ecology (NIOO-KNAW) and at the Aquatic Ecology and Water Quality Management group at Wageningen University.

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